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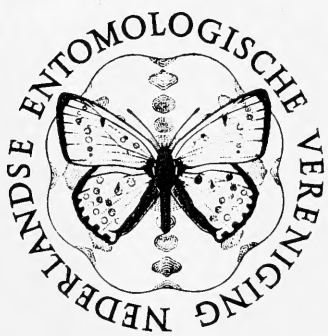


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## ERRATUM

P. 219: 2nd line of summary, "with (*hippophorbiae* × *euphorbiae*) ♀." ..  
should read "with (*hippophorbiae* × *hippophaes*) ♀."

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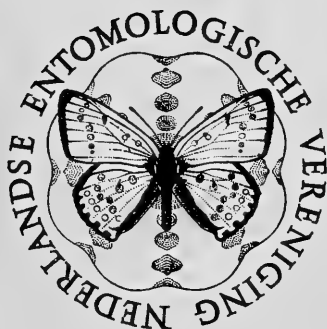
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## INHOUD

- P. F. VAN HEERDT, B. BLOKHUIS and CAROLINE VAN HAAFTEN. — The reproductive cycle and age composition of a population of *Pterostichus oblongopunctatus* (Fabricius) in the Netherlands (Coleoptera: Carabidae), p. 1—13, fig. 1—4, pl. 1—2.





# THE REPRODUCTIVE CYCLE AND AGE COMPOSITION OF A POPULATION OF *PTEROSTICHUS OBLONGOPUNCTATUS* (FABRICIUS) IN THE NETHERLANDS (COLEOPTERA: CARABIDAE)

by

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With two plates and four text-figures

## ABSTRACT

The reproduction of a Dutch population of *Pterostichus oblongopunctatus* (F.) is analysed. Seasonal variations in egg numbers, "corpora lutea" sizes, the relative positions of eggs in ovarioles and oviducts, and the conditions of the eggs were studied. Three age classes (corresponding with one-, two-, and three-year-old females) could be distinguished by measuring the sizes of the "corpora lutea". The duration of the reproduction and its course could be established. The survival value of a population consisting of more than one age class is discussed.

## INTRODUCTION

Previous observations by Den Boer (1968) and Van Dijk (1973) provided information on the heterogeneity of the reproductive cycle which, in some species of carabid beetles, may be important to survival under adverse environmental conditions.

This heterogeneity, which presumably is partly genetically fixed, may contribute to spreading the risk of extinction of the population. Den Boer and Van Dijk observed that not only one-year-old females of *Calathus* species contributed to reproduction, but also two- and even three-year-old ones. These authors observed that in young females at the start of the development of the ovaries no "corpora lutea" (abbreviated c. l.) were present and that only after several weeks the first c.l. could be found. Their results suggest that it would be possible to discriminate between females of the old and the new generation in a field population by means of the c.l. in the ovaria.

The present work was started to investigate the validity of these facts also for *Pterostichus oblongopunctatus*, a carabid beetle common in woods in the Netherlands. The reproductive pattern has been studied by observation of the development of the ovaries and the maturation of the eggs. These features have been studied during a number of successive years in order to unravel the complex dynamics of the population concerned.

The area where the population of *P. oblongopunctatus* has been studied, occupies 2.4 hectares and was planted with oak (*Quercus robur*) about 90 years ago. The oaks are sparsely intermingled with birch (*Betula spec.*) and have formed a dense canopy over a well-developed shrub-stratum. Herbaceous growth is practically non-existent, but a thick layer of partly decomposed leaf-litter (5-10 cm) makes a good hiding place for a rich epedaphic fauna.

#### MATERIAL AND METHODS

*Pterostichus oblongopunctatus* (F.), a small bronze-black coloured beetle (9-12 mm) lives as an adult in the superficial layer of leaf-litter, preferably in broadleaved woods. The larvae usually develop in the deeper layers. Reproduction occurs in spring, the eggs are deposited in the litter.

Pitfall traps (Den Boer, 1968) were used for sampling: a plastic funnel (16 cm) fitted to a glass jar filled partially with 4% formaldehyde and dug into the soil, the rim of the funnel being flush with the soil surface. A cover (Ø 25 cm) is placed 5 cm above the funnel to prevent rain from penetrating into the trap and diluting the formaldehyde. Three units of five traps each were dug in. Once a week the jars were changed for fresh ones, and the specimens of *P. oblongopunctatus* selected from the contents of these jars.

Fresh ovaries proved to be preferable for this study to those preserved in formaldehyde, but the former were available only during 1972. The females were dissected carefully and the ovaries (Fig. 1) were taken out. The development of the ovary and the absence or presence of the corpora lutea are a criterion to the age of the female.

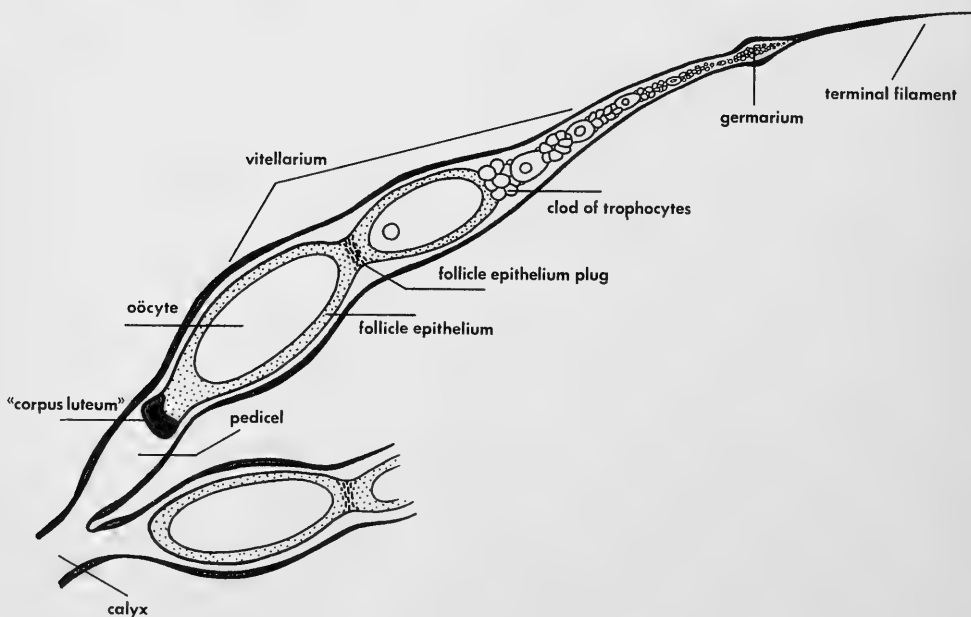


Fig. 1. Ovariole of *Pterostichus oblongopunctatus*, with indication of elements

## RESULTS

In the Netherlands, this species has one generation annually. The newly hatched adults hibernate as virgins, and copulate in spring and summer. The new generation appears in autumn. Thus the activity pattern of the population shows two distinct periods in spring and in autumn (Fig. 2). The spring activity starts in

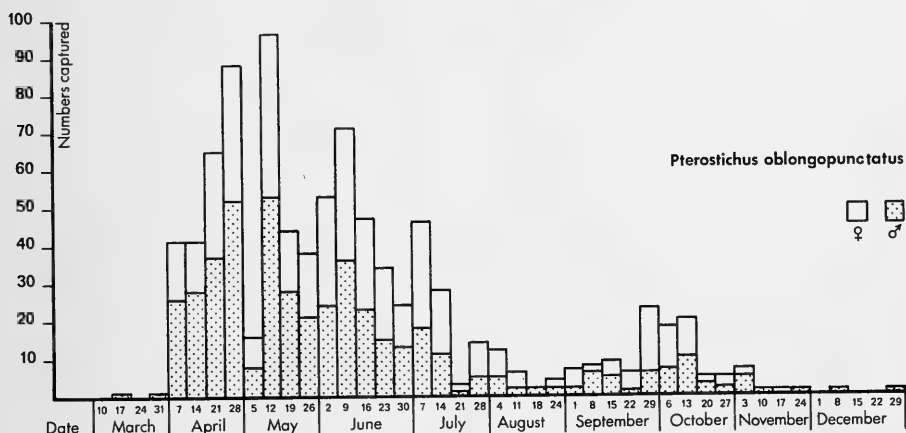


Fig. 2. The activity of *Pterostichus oblongopunctatus* in 1971

approximately the first week of April and is related to reproduction. The number of beetles caught gradually diminishes towards the end of the reproduction period, i.e. the beginning of August. The appearance in September of the new generation probably stands for the major part of the higher catches in autumn. "Spent" females (i.e. those that have oviposited) represent one-third of the specimens trapped, as their activity is low at this time. Until the end of May more males than females are caught (1971: 260 against 189). Presumably the former are more active in this period, in search for a partner. From about the end of May until the first weeks of August the females make up the majority (154 against 186).

The following categories of ♀ in the different stages of development were recognized (Pl. 2):

- Without eggs and without c.l.
- With eggs, without c.l.
- With eggs under the c.l.
- With eggs under and above the c.l.
- With eggs above the c.l.
- Without eggs, with c.l. ("spent").

In the females without c.l. in April, the eggs are still above the calyx, in the ovarioles: a few ♀ (Pl. 2, punctated yellow) have eggs in the calyx, but have c.l. not yet visible. Many ♀ with c.l. are bearing their eggs at this time already under the c.l. in the calyx. The females with c.l. but without eggs may have finished oviposition at this moment ("spent"). The data suggest that at the start of the reproduction season females with c.l. (Pl. 2, gray) may start earlier to reproduce than females without c.l. (i.e. those belonging to the new generation).

According to Vlijm & Van Dijk (1967) it is possible to determine the age of the females by the development of the ovary and the absence or presence of corpora lutea, as follows:

First year ♀:

- |  |   |                     |
|--|---|---------------------|
| (1) an ovary in a state of early development   | } | before reproduction |
| (2) a small, pointed ovary   |   |                     |
| (3) a calyx, not yet elongated   |   |                     |
| (4) without corpora lutea  | } | during reproduction |
| (5) thin, yellowish-brown c.l.   |   |                     |
| (6) thin, but distinct, dark coloured c.l. only at the end of the reproduction period: "c.l. 2". |   |                     |

2nd- or 3rd year ♀:

- (1) thin, dark coloured c.l. before the reproduction period ("c.l. 2")
- (2) distinct, dark coloured c.l. at the beginning of the reproduction period ("c.l. 2")
- (3) big c.l. during the reproduction period ("c.l. 3")
- (4) fat, "fluffy" ovaries (the eggs and ovaria are crumbling and show a fluffy structure).

Since the size of the c.l. has been estimated, it is hard to give a good classification. Especially in specimens with distinct c.l. in the middle of the reproduction period one may be uncertain of their age. In a later stage of research, however, one of us (Blokhuys) used an ocular-micrometer to measure the size of the c.l. Thus more accurate data could be obtained on the difference in size of the c.l. than by mere judgement of their dimension.

The data collected of every female captured in order to judge its stage in the reproduction (Table 1) are as follows:

- (1) the number of ♀ without c.l. or eggs (I)
- (2) the number of ♀ without c.l. with eggs (II)
- (3) the number of ♀ with c.l. and with eggs (III, IV, IVa)
- (4) the number of ♀ with c.l. without eggs ("spent") (V)
- (5) size and colour of the c.l.
- (6) the number of eggs in relation to their position in the ovary
- (7) the condition of eggs and ovaries.

Table 2 shows the relation between the number of eggs per female and the size of the c.l. If the size of the c.l. is a measure for the age of the female, it should be possible to find a relation between age and number of eggs. The number of ovarioles varies between 10-26. The average weekly number is about 15.4-20.0. Probably this number is too low, as counting is made difficult by the "fluffy" ovaries. Three females had few c.l. (resp. 3, 3 and 2) but many ovarioles (14, 18 and 20). In 5 females only one ovary had developed; in 2 females a double c.l. ring could be observed.

#### Development of the corpora lutea.

As Miss Van Haaften (in 1970) and Blokhuys (1971) obtained almost identical results, these can be summarized as follows:

Table 1. 1971: week 1—4: April; 5—8: May; 9—13: June; 14—17: July; 18—25: Aug.; 22—26: Sept.; 27—30: Oct.; 31—35: Nov.; 36—39: Dec. I, number of ♀ without c.l., without eggs; II, number of ♀ without c.l., with eggs; III, number of ♀ with small c.l. (c.l. 1) with eggs; IV, number of ♀ with distinct c.l. (c.l. 2) with eggs; IVa, number of ♀ with large c.l. (c.l. 3) with eggs; V, number of ♀ with c.l. 1, c.l. 2, c.l. 3 without eggs ("spent"). Between brackets: percentages I-II (without c.l.); III (c.l. 1); IV (c.l. 2); IVa-V (c.l. 3) of the total of animals caught

Week 1971	I		II		III		IV		IVa	V			IVa + V %
	nr.	%	nr.	%	nr.	%	nr.	%		c.l. 1	c.l. 2	c.l. 3	
1	5	2 (47)	—	—	2	(13)	1	—	—	—	—	5	(40)
2	6	2 (67)	—	—	2	(16.5)	2	—	—	—	—	—	(16.5)
3	4	9 (48)	—	—	7	(26)	5	—	—	—	—	2	(26)
4	2	10 (33)	4	(11)	11	(31)	6	—	—	—	—	3	(25)
5	—	1 (12.5)	3	(37.5)	2	(25)	2	—	—	—	—	—	(25)
6	3	8 (27)	15	(37)	8	(22)	5	—	1	1	—	1	(14)
7	—	5 (31)	6	(37)	3	(19)	2	—	—	—	—	—	(13)
8	1	4 (30)	6	(35)	4	(24)	2	—	—	—	—	—	(11)
9	—	9 (31)	11	(41)	4	(14)	4	1	—	—	—	—	(14)
10	—	7 (20)	15	(46)	6	(17)	5	1	—	—	—	1	(17)
11	1	3 (16)	12	(54)	2	(14)	4	1	1	—	—	—	(16)
12	—	—	14	(74)	2	(16)	2	—	1	1	—	1	(10)
13	—	—	6	(55)	1	(18)	2	—	1	1	—	1	(27)
14	3	— (11)	12	(43)	4	(21)	3	—	2	4	—	—	(25)
15	1	— (6)	9	(53)	3	(18)	—	—	—	—	—	4	(23)
16	1	— (50)	—	—	1	(50)	—	—	—	—	—	—	—
17	—	—	1	(11)	5	(56)	—	—	—	—	—	3	(34)
18	1	— (14)	—	—	3	(43)	1	—	—	—	—	2	(43)
19	—	—	1	(25)	—	—	—	—	—	—	—	3	(75)
20	—	—	—	—	—	—	1	—	—	—	—	—	(50)
21	1	— (50)	—	—	—	—	—	—	1	—	—	—	(50)
22	2	— (40)	—	—	—	—	—	—	—	—	—	3	(60)
23	1	— (50)	—	—	—	—	—	—	—	—	—	1	(50)
24	3	— (75)	—	—	—	—	—	—	1	—	—	—	(25)
25	5	— (100)	—	—	—	—	—	—	—	—	—	—	—
26	13	— (76)	—	—	—	—	—	2	—	—	—	2	(24)
27	8	— (73)	—	—	—	—	—	—	1	2	—	—	(27)
28	7	— (70)	—	—	—	—	—	1	2	—	—	—	(30)
29	1	— (33)	—	—	—	—	—	—	—	—	—	2	(77)
30	1	— (50)	—	—	—	—	—	1	—	—	—	—	(50)
31	1	— (50)	—	—	—	—	—	1	—	—	—	—	(50)
32	—	—	—	—	—	—	—	—	—	—	—	—	—
33	1	— (100)	—	—	—	—	—	—	—	—	—	—	—
34	—	—	—	—	—	—	—	—	—	—	—	—	—
35	—	—	—	—	—	—	—	—	—	—	—	—	—
36	—	—	—	—	—	—	—	—	—	—	—	—	—
37	—	—	—	—	—	—	—	—	—	—	—	—	—
38	—	—	—	—	—	—	—	—	—	—	—	—	—
39	1	— (100)	—	—	—	—	—	—	—	—	—	—	—
	73	60			115		70		46	9	11	39	

Table 2. 1971. The relation between the number of eggs per ♀ and the size of the c.l.; II, no c.l.; III, small c.l. (c.l. 1); IV, distinct c.l. (c.l. 2); IVa, large c.l. (c.l. 3)

Number of eggs per ♀	II	III	IV	IVa
1	1	2	8	2
2	1	—	17	10
3	1	1	13	10
4	3	6	7	4
5	3	2	6	3
6	6	11	5	3
7	5	10	2	1
8	8	15	1	5
9	9	16	3	2
10	3	9	2	1
11	6	5	1	—
12	6	4	1	1
13	6	7	1	2
14	1	9	—	1
15	—	4	1	1
16	—	7	1	—
17	1	2	—	—
18	—	2	1	—
19	—	—	—	—
20	—	2	—	—
21	—	—	—	—
22	—	1	—	—
Number of ♀	60	115	70	46
Number of eggs	526	1153	326	243
Mean number of eggs	8.8	10.0	4.7	5.3

In the second week of April females without c.l. still constitute 44-67% of the total catch. Their numbers decrease gradually to zero — after July 14 the results are unreliable. Females with c.l. 1 are observed for the first time in the last week of April. Their share begins with 6—11% and rises to 74% in the third week of June. Later the numbers decline again, but apparently more gradually than is suggested by Table 1, for it has to be corrected by those females which have grown from c.l. 1 to c.l. 2. The resulting decline is probably caused by a decrease of activity. The number of females with c.l. 2 attain a maximum in April (30%). After April 28 their number decreases, because either their c.l. 2 may grow to c.l. 3 or by mortality of the supposed 2nd year individuals. The number of females with c.l. 3: this group is at the onset of the activity represented to 40%, but as April wears on their numbers decrease rapidly to 20%, in May even to 11%. After May 26 an increase takes place again, apparently as a consequence of c.l. 2 ♀ developing into c.l. 3 individuals as they continue to produce eggs. The initial decrease is, obviously, caused by the dying off of the supposed 3rd year generation (Pl. 2). It must be noted that the first females with eggs beneath the c.l. (April) are of the c.l. 3 group, hence, the oldest females apparently take the lead in reproduction, but within a few weeks they are already “spent” again and will probably die off soon,

Table 3. 1972. Size of the c.l. measured in  $\mu$ 

<i>From 30 March to 12 April</i>		<i>From 31 May to 14 June</i>	
Size	Number ♀	Size	Number ♀
— <sup>1)</sup>	19	—	2
83 $\mu$	2	23 $\mu$	1
85 $\mu$	2	31 $\mu$	3
108 $\mu$	2	42 $\mu$	1
112 $\mu$	1	45 $\mu$	2
123 $\mu$	1	46 $\mu$	4
		49 $\mu$	1
		77 $\mu$	2
		88 $\mu$	1
		92 $\mu$	2
		97 $\mu$	1
<i>From 12 April to 26 April</i>		<i>From 14 June to 28 June</i>	
Size	Number ♀	Size	Number ♀
—	80	—	2
31 $\mu$	1	29 $\mu$	1
49 $\mu$	1	31 $\mu$	1
54 $\mu$	3	40 $\mu$	1
62 $\mu$	2	46 $\mu$	1
120 $\mu$	1	49 $\mu$	1
		50 $\mu$	1
		54 $\mu$	1
		55 $\mu$	1
		57 $\mu$	1
		62 $\mu$	10
		69 $\mu$	3
		72 $\mu$	1
		77 $\mu$	7
		108 $\mu$	1
		123 $\mu$	2
		131 $\mu$	1
<i>From 26 April to 10 May</i>		<i>From 28 June to 12 July</i>	
Size	Number ♀	Size	Number ♀
—	9	—	0
28 $\mu$	1	46 $\mu$	1
31 $\mu$	3	69 $\mu$	1
54 $\mu$	1	77 $\mu$	4
62 $\mu$	2	123 $\mu$	1
69 $\mu$	1		
77 $\mu$	1		
<i>From 10 May to 31 May</i>			
Size	Number ♀		
—	11		
31 $\mu$	2		
38 $\mu$	1		
42 $\mu$	1		
58 $\mu$	1		
62 $\mu$	2		
69 $\mu$	1		
92 $\mu$	3		
108 $\mu$	1		

<sup>1)</sup> — = without c.l.

according to their disappearance in May (Pl. 2). A postponed reproduction of the preceding year may be possible, so that 2nd year ♀ may die when they are two years old and only those ♀ which failed to reproduce the previous year would reach their 3rd year (Vlijm & Van Dijk, 1967, have supposed this to be the case in *Calathus melanocephalus*).

Measurements of corpora lutea.

The estimate of the size of the c.l. being not quite reliable, those of freshly

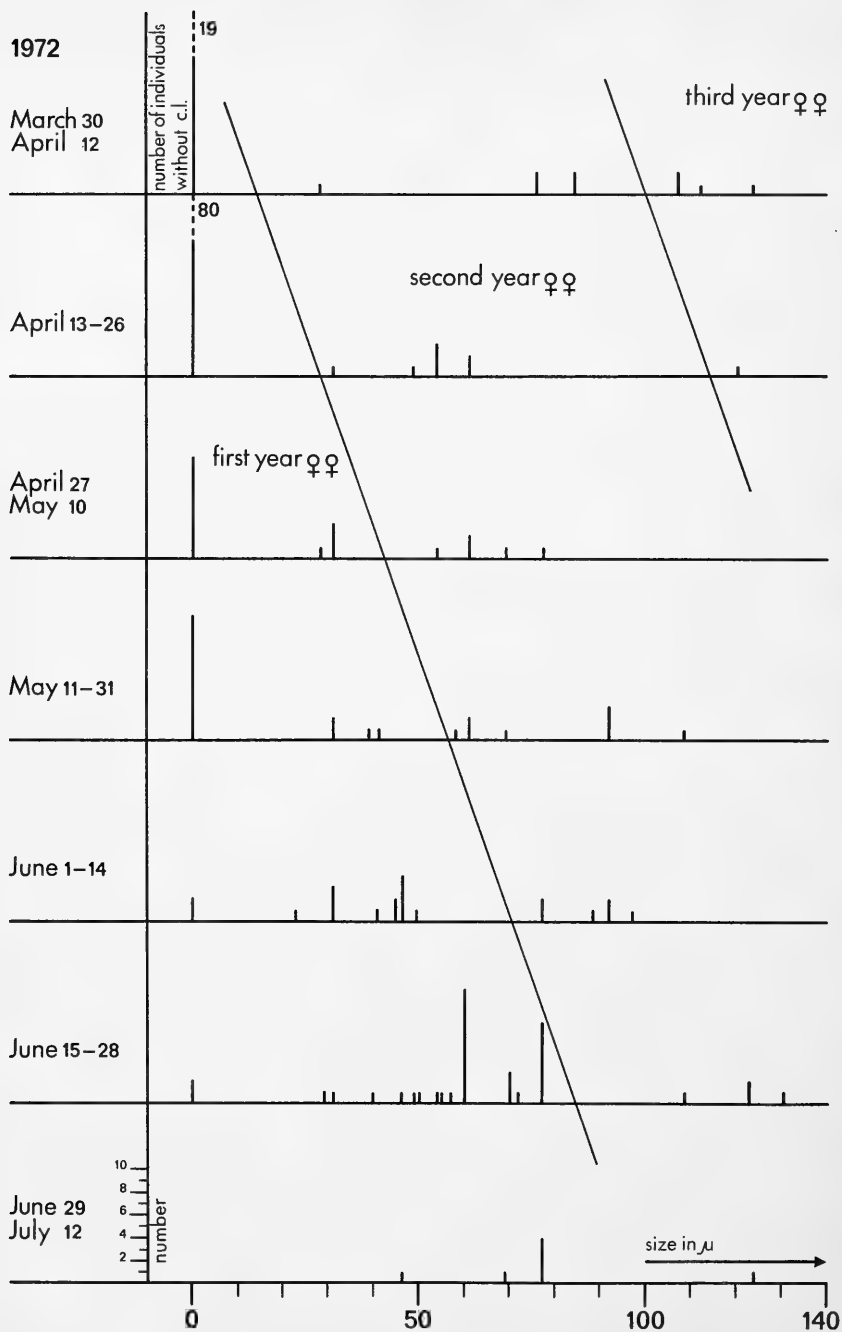


Fig. 3. Size of corpora lutea in 1972



caught ♀ were measured by Blokhuis in 1972 by means of an ocular micrometer at a magnification of  $100\times$  (Table 3). In the first weeks of April 1972 only females with c.l. 3 ( $108\text{--}124\mu$ ) or large c.l. 2 ( $77\text{--}85\mu$ ) were present. One female with a c.l. of  $28\mu$  probably reproduced only a short time during the preceding year. In the second half of April only one ♀ with c.l. 3 was captured, but females with small c.l. 2 made their first appearance ( $50\text{--}60\mu$ ). No females with c.l. 3 could be caught during the first part of May but the c.l. of the c.l. 2 females tend to be bigger ( $55\text{--}80\mu$ ) and it is in this period that females with c.l. 1 have been collected for the first time. During the second part of May, in June and the first two weeks of July the c.l. 2 have reached the size which the c.l. 3 showed in April, and the c.l. 1 those of the c.l. 2. During 7 weeks (April 26–June 14) not a single female with c.l. 3 had been caught. Hence, we may conclude that females with c.l. 3 at the onset of the breeding season (first half of April) die after oviposition. The new 2nd year females take their place at the end of June. These data are a confirmation of the hypothesis that more generations are involved in reproduction (Fig. 3).

A check in 1973 on individuals of the 1971 generation which were marked as young females in 1972, showed a size of the c.l. corresponding with those of second year ♀ (cf. Fig. 4). Consequently the age of a female can be estimated approximately by these figures though a certain overlap exists. It is evident that at a certain moment of development, 1st year c.l. 2 and 2nd year c.l. 2 do not differ in

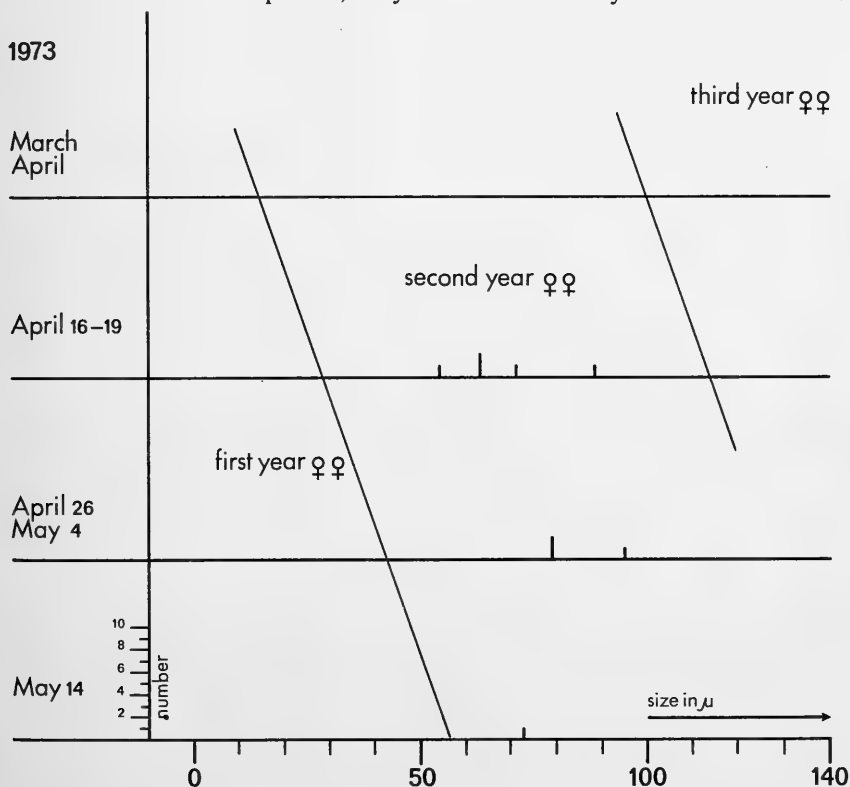


Fig. 4. Size of the corpora lutea of individuals marked in 1972, recaptured in 1973

size. A more accurate way to determine the ages of the ♀ taking part in reproduction is the marking-recapture method which we intend to use in the future.

A serious obstacle in the interpretation of "corpora lutea" (sizes as well as numbers) as indicators of age is the phenomenon of egg resorption (Joly, 1949, and others). The precise origin of the c.l. seems to be unknown.

#### Egg production.

When dissected, only 6 out of the 291 egg-bearing females appeared to have white, glossy, elastic eggs, one female had brown, hard, malformed eggs. The eggs of all the other females proved to be "fluffy" and soft and were coloured light yellow to orange. It is possible that this coloration is due to the preservation agent, i.e. formaldehyde.

In the first week of May all females are bearing eggs. This situation is reached within one month. Decrease to zero takes more time: it takes more than 3 months before the last egg has been deposited (Table 4).

Table 4. 1971. The number of egg bearing ♀. Week nr. 1: March 31-April 7. Week nr. 20: August 11-August 18

Week	Total ♀	♀ + eggs	%
1 31 March	—	—	—
2 7 April	15	5	33
3 14 April	12	6	50
4 21 April	27	21	78
5 28 April	36	31	86
6 5 May	8	8	100
7 12 May	43	36	84
8 19 May	16	16	100
9 26 May	17	16	94
10 2 June	29	28	97
11 9 June	35	33	94
12 16 June	24	21	88
13 23 June	19	18	95
14 30 June	11	9	82
15 7 July	28	19	68
16 14 July	17	12	71
17 21 July	2	1	50
18 28 July	9	6	67
19 4 Aug.	7	4	57
20 11 Aug.	4	1	25

In 1971, the average number of eggs was 7.7. Computing the number for each group of females shows that females without c.l. and those with small and thin c.l. have an average of 9.6 eggs; c.l. 2 females have 4.6 and c.l. 3 females 5.8 (Table 5). It can thus be concluded that the females without c.l. and with c.l. 1 produce the majority of the eggs. The groups with c.l. 2 and c.l. 3 contribute only one third of the total.

By means of Wilcoxon's Two Sample Test the zero-hypothesis of a similar egg-

Table 5. The average number of eggs in 1970 and 1971

	1970	1971	Corrected average numbers (1971)
Generation 1967 } Generation 1968 }	5.5	5.8	(6.3 for c.l. 3-group ♀ in April)
Generation 1969	4.3	4.6	(4.7 for c.l. 2-group ♀ and c.l. 3-group ♀ without in April)
Generation 1970	—	9.6	

N.B. Generation 1968 corresponds with the c.l. 3 group in April 1971. Generation 1969 corresponds with the c.l. 2 group and the c.l. 3 group together, without the individuals with c.l. 3 caught in April. Between brackets the corrected averages of the number of eggs. After April the c.l. 3 group should be added to the c.l. 2 group because of the development of c.l. 2 to c.l. 3 in the course of the summer. The average of 5.5 has been computed by adding the number of eggs of the generations 1967 and 1968 which until that time could not yet be discerned. Only the c.l. 3 ♀ caught in April probably have an age of three years (or more).

production in two groups is tested against the alternative hypothesis of a different egg-production ( $\alpha = 0.05$ ;  $u = 1.96$ ). It can be concluded that group II and III do not differ significantly. This could be expected as these groups belong to the same generation: 1970-groups II and IV differ significantly ( $u = 6.4$ ;  $p < 0.0001$ ) as do groups II and IVa ( $u = 4.76$ ), but groups IV and IVa do not differ significantly ( $u = 1.22$ ).

Miss van Haaften, in 1970, arrived at the same results with the Median Test.

## CONCLUSIONS AND DISCUSSION

### Composition of the population.

The results show that the population consists of 3 generations which are all nearly simultaneously active (Table 6, which has been derived from Tables 1 and 5). In June and July only 2 generations are present, as the 3rd generation dies off after oviposition in April-May and the new generation hatches only in September.

### Survival value.

As the larval stage is supposed to be rather vulnerable, it is evident that, if one generation in its larval stage is severely damaged by adverse environmental (humidity or temperature: too high or too low) and/or biotic (disease, parasites, predators) influences, the next year still two additional generations survive to assure the persistence of the population: the last 4 years about 40% of the females taking part in reproduction consisted of 2 or 3 year old (Table 7).

At the beginning of 1971 (March 31-May 5), the rate of 2nd and 3rd year egg-bearing females stood at 44%, the total number captured, i.e. 2nd and 3rd year ♀ without eggs included, even at 51%. As reproduction goes on these numbers decline respectively to 25% ♀ with eggs and to 24% of all females captured in the period May 6-June 2 and to 30% ♀ with eggs and 36% ♀ of all ♀ captured in the period June 3-July 7.

The ratio of this last period is too high owing to a failure in the correct estimation of the size of the c.l. which in the future can be eliminated by the micrometer method (cf. p. 9).

Table 6. Reproductive activity in 1971

Date	Age	Reproductive activity	Generation
April	1st year	without c.l., without eggs	1970
	1st year	without c.l., with eggs	1970
	1st year	with c.l. 1, with eggs	1970
	2nd year	with c.l. 2, with eggs	1969
	3rd year	with c.l. 3, with eggs	1968
	3rd year	with c.l. 3, "spent"	1968
May	as April	but 3rd year ♀ disappear	
June	1st year	with c.l. 1, with eggs	1970
	1st year	spent with c.l. 1 and c.l. 2	1970
	2nd year	with c.l. 3 and eggs	1969
	2nd year	spent with c.l. 3	1969
July	1st year	with c.l. 1, c.l. 2 and eggs	1970
	1st year	spent with c.l. 2	1970
	2nd year	spent with c.l. 3	1969
August	1st year	with c.l. 2 and eggs	1970
	1st year	spent with c.l. 2	1970
	2nd year	spent with c.l. 3	1969
September	Hatching of the new	generation	1971
	1st year	spent with c.l. 1 and c.l. 2	1970
	2nd year	spent with c.l. 3	1969
October	New generation		1971
	1st year	spent with c.l. 1	1970
	2nd year	spent with c.l. 3	1969

The first year generation (1970) produced a large number of eggs (average 9.6). The second year generation (1969) had an average production of 4.7, the third year generation (1968) one of 6.3. According to Miss Van Haaften, the generations of 1969 and 1968 produced about the same average (4.3 and 5.5, respectively). Data of 1972 have already confirmed that the population increased with about 10%: the generation of 1970 may have had a big part in this increase.

Survival, however, is not dependent of meteorological factors only: predation, disease and the available amount of food will be important too, but reliable data are, thus far, lacking.

#### Comparison with other carabid beetles.

It is a special advantage that Van Dijk (l.c.) studied the age composition of *Calathus melanocephalus* (L.) which is, contrary to *P. oblongopunctatus*, a "winter

Table 7. Composition of the population in 1969, 1970 and 1971

Year	Locality	% more than one year old	Method
1969	Baarn	49%	by estimating the size of the c.l. (by De Bruyn)
1970	Baarn	32%	by estimating the size of the c.l. (by Van Haaften)
1971	Baarn	39%	by estimating the size of the c.l. (by Blokhuis)
1969	Wijster	37%	capture-recapture (Van Dijk, personal communication)

breeder" (i.e. the larvae develop during winter time). In the former species young adults hatch in spring and only mature in the course of July, while in *P. oblongopunctatus* the adults hatch in September, mature in the course of the autumn and start oviposition towards the end of April. In *P. oblongopunctatus*, egg-production by 1st year females as well as by 2nd and 3rd year females starts earlier in the season but finishes about July 21, whereas in *C. melanocephalus* it continues well into September. As a matter of fact, *P. oblongopunctatus* has a lead over *C. melanocephalus* as at a certain moment (end of April, beginning of May) three generations may reproduce simultaneously, contrary to *C. melanocephalus* where at best two generations do so.

#### ACKNOWLEDGEMENTS

We are grateful to Dr. P. J. den Boer and Dr. T. S. van Dijk (Dr. W. Beyerinck Biologisch Station, Wijster) for their stimulating interest and useful advice in our investigations. We thank Dr. W. J. Sluiter for reading the manuscript and Miss M. A. de Bruyn for putting some preliminary results at our disposal.

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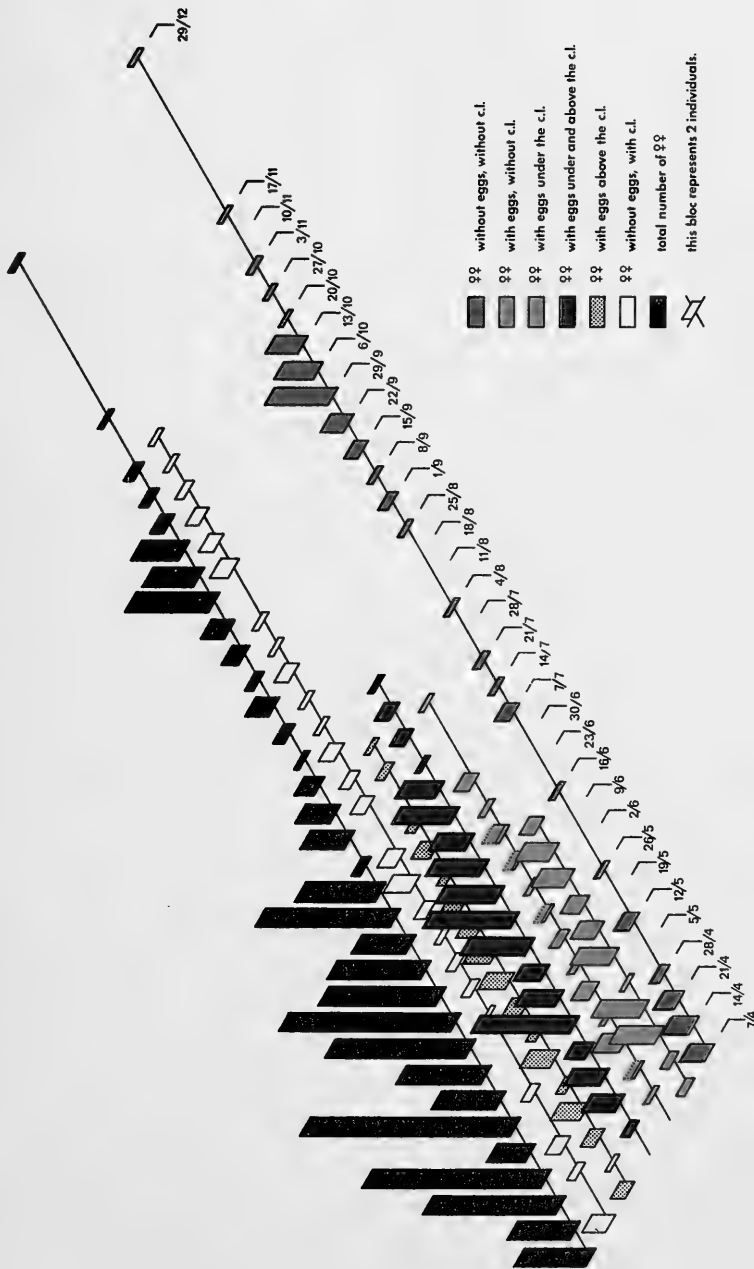
*a*

*b*

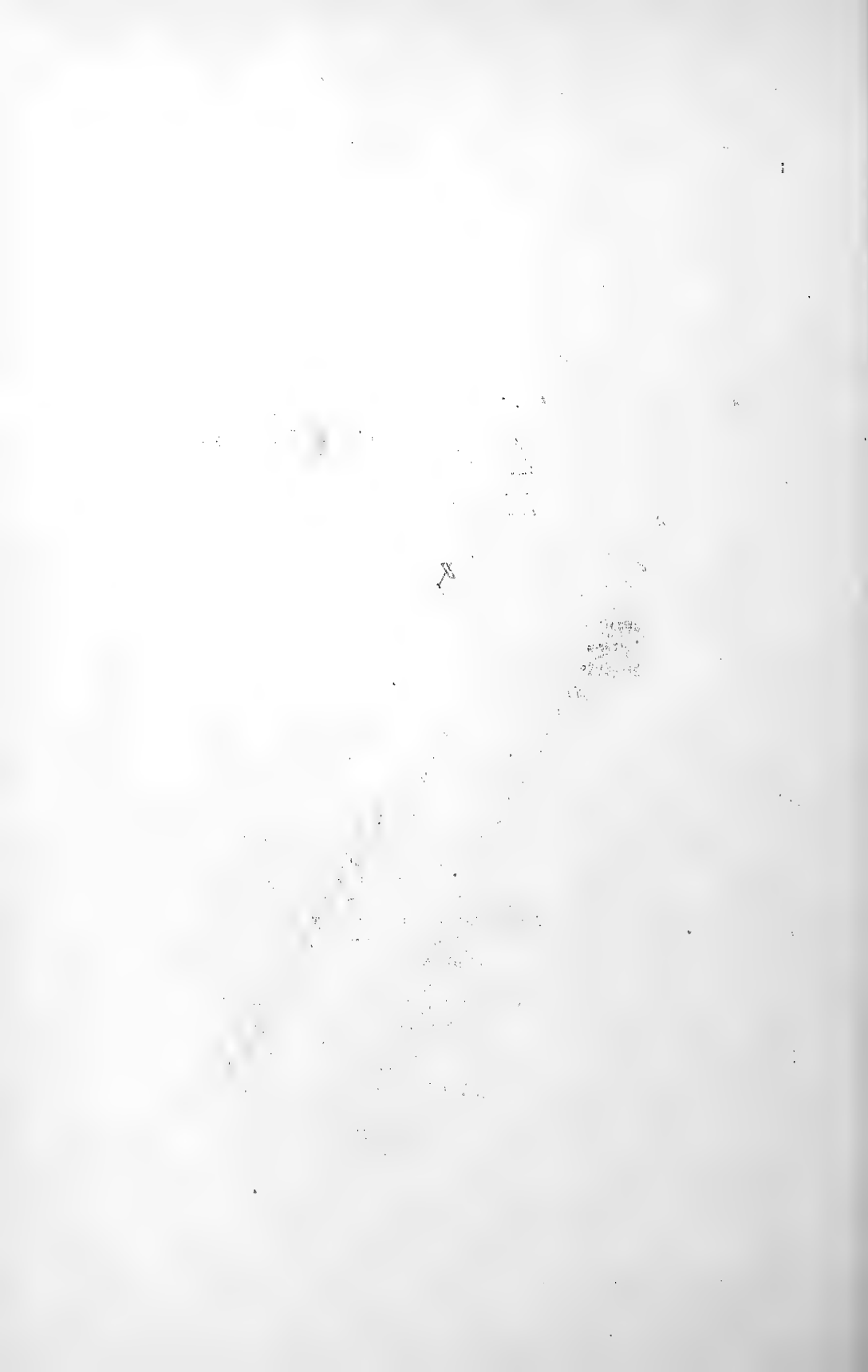
Ovaria and oviducts of *Pterostichus oblongopunctatus*. a, corpora lutea; b, egg in pedicel







Survey of the reproductive cycle in 1971







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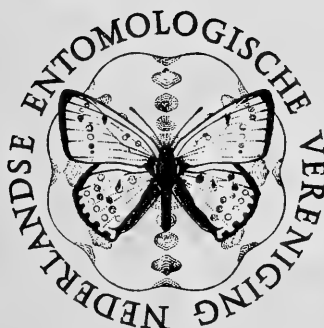
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- P. STELLEMAN and A. D. J. MEEUSE. — Anthecological relations between reputedly anemophilous flowers and syrphid flies. I. The possible role of syrphid flies as pollinators of *Plantago*, p. 15—31, fig. 1—2, pl. 1—3.



# ANTHECOLOGICAL RELATIONS BETWEEN REPUTEDLY ANEMOPHILOUS FLOWERS AND SYRPHID FLIES

## I. THE POSSIBLE ROLE OF SYRPHID FLIES AS POLLINATORS OF *PLANTAGO*

by

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With two figures and three plates

### ABSTRACT

Regular visits by syrphid flies of the genera *Melanostoma* and *Platycheirus* to the inflorescences of the reputedly anemophilous *Plantago lanceolata* L. for the purpose of pollen consumption have often been reported. An effective pollen transfer could be established in the present study. Observations made in the field indicated that the flies feed on *Plantago lanceolata* pollen in the early morning. Several aspects of their behaviour already suggest them to be effective pollen vectors. By means of Scanning Electron Microscope observations the presence of pollen grains of *P. lanceolata* on the body of the flies could be demonstrated. Experiments in which artificially dyed pollen of *P. lanceolata* was deposited on inflorescences in anthesis, while the stained pollen was subsequently recovered from the stigmas of other spikes, demonstrate that they are efficient pollinators of this plant. The amount of pollen transferred was estimated and, at least in certain habitats, is thought to be responsible for a considerable part of the geitonogamous and heterogamous pollinations. The technique employed may prove to be useful for the study of comparable cases in plants and animals.

### I. OBSERVATIONS IN THE FIELD AND PRELIMINARY STUDIES

The taxon Syrphidae (Diptera) almost exclusively consists of species which in the adult stage are typically anthophilous and feed chiefly on pollen or nectar. Differences in body size, and in the length of the proboscis, are considerable, so that a rather wide range of flowers can be visited. Among the Diptera, the Syrphidae are in general the most important pollinators, although their significance is not as great as that of the social hymenopterous group of the Apidae (Kugler, 1970; Faegri & Van der Pijl, 1971).

As may be expected, syrphid flies normally visit flowers or inflorescences of typically entomophilous plants, but observations in the field have shown that some reputedly anemophilous plants are visited regularly by various species of Syrphidae for the purpose of pollen consumption. However, the published records provide relatively few reliable data. The most important ones, to be mentioned presently, refer mostly to visits by representatives of the closely related genera *Melanostoma* and *Platycheirus* of the subfamily Syrphinae.

One of the earliest reports is by Müller (1873), who noted that in the surroundings of Lippstadt (W. Germany) insects often gather or consume pollen on the spikes of *Plantago lanceolata*. Beside Hymenoptera, he reported several

Syrphidae among which *Melanostoma mellinum* (Linnaeus) is specially mentioned as a frequent pollen-eating visitor. Müller pointed out that this fly even shows a preference for wind-pollinated flowers: he found this insects as a regular pollen consumer on *Plantago media* L., *Artemisia dracunculus* L., *Scirpus lacustris* L., and several grasses such as *Anthoxanthum odoratum* L., *Poa annua* L., and *Festuca pratensis* Huds. It was also found on a whole range of entomophilous plants where, apart from pollen, it sometimes also ingested nectar. Müller believed that visits to anemophilous plants by this type of insects might result in cross-pollination. Representatives of the closely related *Platycheirus* were not reported as visitors of wind-pollinated taxa.

Ludwig (1881, 1884) noticed a very large number (several thousands) of syrphids of the genera *Melanostoma*, *Platycheirus* and *Melithreptus* (*Sphaerophoria*) on the panicles of *Molinia coerulea* (L.) Moench in Saxony (E. Germany). An appreciable number were caught by the proboscis between the paleae or the anthers and in that case they usually appeared to be infected by a parasitic fungus (*Entomophthora* spec.), while living flies were often found to be present also. Ludwig suggested that the purplish-mauve colour of the anthers acts as a strong attractant for the visitors. He observed the same flies on *Phleum pratense* L., *Helictotrichon pubescens* (Huds.) Pilger, *Dactylis glomerata* L., and *Plantago lanceolata*.

The extensive monograph of Knuth (1898—1905) records a number of cases of *Melanostoma mellinum* visiting various anemophiles. Apart from citing earlier authors he also reported personal observations made near Kiel and in the North Frisian islands (W. Germany), where he frequently noted several specimens of this fly on inflorescences of *Alopecurus pratensis* L., *Phleum pratense*, and *Anthoxanthum odoratum*. He also mentioned visits of this species to *Plantago arenaria* W. & K. (in a botanical garden) and to *Sanguisorba minor* Scop. Knuth did not attribute any significant role to these visits in effective pollen transfer. In addition he mentioned an appreciable number of visits of *Melanostoma mellinum* (and other species of the genus) and of *Platycheirus* species to entomophilous flowers.

Drabble & Drabble (1927) reported that at one time (in Great Britain) they saw inflorescences of *Phleum pratense* literally covered with *Melanostoma mellinum* and *Hylemia variata* (Fallén) (Diptera, Anthomyiidae), which were busy gathering pollen. They believed that these insects are undoubtedly effective pollinators. *Dactylis glomerata* was also visited for foraging purposes but its inflorescences do not seem to be as attractive as those of other grasses.

Porsch (1956) gave an extensive survey of Coleoptera and Diptera recorded as pollen consumers on anemophilous plant species, but his lists are chiefly compiled from earlier publications and do hardly contribute any new data on syrphids.

For our present study the publication by Van der Goot & Grabandt (1970) proved to be important. They studied the pollen content of the digestive tract of several anthophilous species of Syrphidae belonging to the genera *Melanostoma*, *Platycheirus*, and *Pyrophaena*. The senior author had repeatedly (in the Netherlands) observed these flies visiting the inflorescences of Gramineae and of *Plantago lanceolata*. In order to assess their possible preference for anemophilous plants the ingested pollen was studied. It appeared that the diet of several species, viz., *Platycheirus clypeatus* (Meigen), *P. fulviventris* Macquart, *P. scambus* (Staeger)



and *P. angustatus* Zetterstedt, consisted almost exclusively, and that of others, such as *Melanostoma mellinum* (L.) and *M. scalare* (Fabricius), partly, of pollen of the above-mentioned anemophiles. (It may be mentioned in passing that Grabandt has found pollen of *Plantago* and of grasses in related syrphids collected in Canada; pers. comm.). In all other species of syrphid flies examined the diet normally consists of pollen of entomophilous plants, anemophilous pollen apparently only being taken occasionally.

All observations cited and pollen analyses clearly indicate a certain degree of consistency in the visits of the *Melanostoma-Platycheirus* group to several anemophiles, more particularly to *Plantago lanceolata* and a number of grasses.

The question arises whether these flies can indeed act as effective pollinators for these reputedly anemophilous plants and if so, what the effectiveness of pollen transfer by insects is in comparison to the anemophilous pollination. As mentioned above, some authors suggest that pollen transfer by insects may be of some importance, but this conclusion is solely based on recorded observations of visits. In our opinion such listings of visitors, although indispensable, are only indicative of a possible pollen transfer, and only an experimental analysis can lead to more definite conclusions. Such an approach has hitherto never been attempted, as far as can be ascertained.

The studies reported in the present paper were primarily intended to demonstrate the possible incidence of an effective pollen transfer by syrphid flies from one inflorescence to another, both through field studies and experimentally. Three methods were employed:

- (1) Field studies, mainly centred around the patterns of behaviour of the syrphids, as far as important in connection with a possible pollen transfer;

- (2) the use of the SEM technique to study the precise localisation of pollen grains attached to the flies after a visit;

- (3) experiments with stained (marked) pollen to demonstrate actual pollen transfer in the field (chapter II).

For practical reasons it was deemed necessary, for the time being, to limit our investigations mainly to *Plantago lanceolata*. The results obtained by Van der Goot & Grabandt (1970) rendered the choice of the potential pollen vectors an easy one; the following and (locally) relatively common species seemed to be the most likely candidates: *Melanostoma mellinum*, *Platycheirus clypeatus*, *P. fulviventris*, and *P. scambus*.

Since it is often impossible to identify each species with certainty in the field, especially flying specimens and those paying a fleeting visit to an inflorescence being hard to recognize, the flies were, generally speaking, treated as a group. This admittedly is a somewhat weak element in our deductions, but we had no option. Exact identification is always possible when the specimen is caught and can be examined, but we refrained from this practice as much as possible. Not only is it a time-consuming procedure, but we also did not want to extract so many individuals from the ecosystem within the scope of our investigations. Identifications of killed specimens were reduced to an unavoidable minimum. Fortunately we have obtained the strong impression from our observations in the field that the behaviour of all species included in our study is very similar, and for the purpose

of the present investigation identical. Whenever the terms "syrphids" or "flies" are used in the following text, unless stated otherwise, always representatives of the *Melanostoma-Platycheirus* group are meant.

The report covers investigations carried out in 1973 and 1974; the field work was carried out from about the beginning of May till the end of September. Low-lying sites near water offered good opportunities. The main areas for study selected were the Naardermeer and (less intensively) the Ankeveen broads. Incidental observations were also made elsewhere in the province of Noord-Holland. The SEM observations were made at the Laboratorium voor Electronenmicroscopie of the University of Amsterdam.

### Observations in the field

Observations in the field indicate that syrphids habitually visit inflorescences of *Plantago lanceolata*. Spikes in the male stage of anthesis (*P. lanceolata* is protogynous) are predominantly visited in the early hours of the morning after sunrise. There is a marked correlation between the beginning of the (male) anthesis and the activity of the flies. Both processes seem to be temperature-dependant and commence in the temperature range between 10°—13°C, but may to some extent also be incited by other factors. As soon as in a population of *P. lanceolata* the male anthesis has begun, i.e., when the first stamens have emerged, a few syrphids begin to arrive and descend on the inflorescences to start feeding on pollen. Normally these events take place between 5.00 and 7.00 hrs, but on relatively cool mornings, or when bad weather conditions prevail, the period may shift to a later time in the morning.

In the beginning the male phase of anthesis develops slowly and the number of visitors remains limited. When the temperature rises and the weather is not too unfavourable, the anthesis rapidly becomes more general and the frequency of the visits also increases appreciably in a short time span. Every day there is a relatively short period of an optimum of visits which seldom exceeds a couple of hours and falls between about 6.00 and 11.00 hrs, but the frequency usually diminishes already before 10.00 hrs and only rarely stays high after 11.00. After the decrease the visits diminish in number, and soon become more or less incidental to cease completely at about 11.00 hrs; the flies become less active after feeding and descend to various parts of plants to rest, but especially in the beginning they often perform cleansing and preening movements with their legs.

The sequential phenomena just described are probably connected with the following circumstances:

(i) More or less constant and at least fairly favourable weather conditions during the early morning induce a certain regularity in both the course of anthesis and the frequency of the visits until the optimum is attained;

(ii) Dissipation of the pollen from the anthers principally by air currents (wind power!) results in the exhaustion of the pollen in the anthers which reduces their importance as a source of food;

(iii) The flies become satiated after having consumed a large quantity of pollen and start their resting phase.

Unfavourable weather in the morning, but sometimes during the previous evening or night, may bring about appreciable deviations from the regular pattern of anthesis and the visiting rhythm. Our observations concerning the male phase of anthesis agree almost completely with the results of Hyde & Williams (1946) obtained at Cardiff (Wales).

Continuous observation of a group of flowering plantains during which all visits were recorded revealed that some of the spikes in anthesis are markedly more frequently visited than most other ones and that a sometimes appreciable number of spikes is not visited at all. The cause of this selective preference is obscure. Quite regularly two or three flies are present on the same spike, but larger numbers are usually not encountered: eight specimens were seen on a single spike on only one occasion.

The pattern of behaviour of the flies suggests that some activities may be of importance for a possible transfer of pollen. This requires some presuppositions, viz.,

- (a) that pollen grains indeed become attached to the body of the fly, and
- (b) that the pollen can subsequently be transferred to the stigmatic area of a different flower.

Some characteristics of behaviour established on the basis of numerous observations are the following.

It appears that as a rule the syrphids fly in the direction opposite to the prevailing movement of the air immediately above the stand of vegetation. This mode of flight was used to advantage in experiments to be described in the second chapter.

The approach flight towards a spike in anthesis is not necessarily followed by a landing on the same spike; quite frequently the insect hovers in the air in front of it for a short while to proceed to a different inflorescence where the movement may be repeated before the fly decides to descend on a third spike, etc. The final landing is preceded by a series of brief thrusting movements aimed at the inflorescence. The fly usually alights directly upon the anther-bearing zones, but not rarely on the portion of the spike above the stamens in which only the female phase of anthesis has proceeded (i.e., on the stigma-bearing zone); in the latter case the fly walks downwards towards the stamen-bearing part of the inflorescence.

When manipulating the anthers to feed on the pollen, the fly is usually attached to some place on the spike by means of its second and third pairs of legs and clutches an anther with its front legs. It subsequently places its proboscis in the dehiscence fissure of a theca and works it over along its full length. As soon as the theca seems to become empty the anther is given a half turn by the front legs so that the opposite slit comes within reach of the tongue. After having thus systematically emptied an anther the fly grabs another one but may also move towards the stigma-bearing zone of the spike or take off. The syrphids seem to prefer freshly dehiscent anthers, but somewhat older ones are also used for foraging, especially later in the morning. Pollen consumption is repeatedly interrupted by preening (preening and cleaning of the body also take place when the insects are resting after feeding as we have seen).

The duration of a single visit to a flowering spike varies considerably. From over 900 observations it could be deduced that visits lasting from less than 30 seconds to 2 minutes constitute about 50% of all visits, and that 87% of the visits do not last longer than 15 minutes. Visits of longer duration were recorded now and then; two exceptional cases of visits, lasting 56 and 58 minutes, respectively, were noted.

During the working over of the anthers the flies may take up different positions. This may be of importance in connection with the possible contamination of the insect body with pollen and in some instances also with the possible deposition of pollen grains adhering to the body on pollen-receptive stigmas. The most characteristic postures are the following:

- (i) the insect sits inside the stamen zone; contamination of different portions of the body with pollen is possible (Pl. 1 Fig. 1);
- (ii) the fly takes up a practically vertical position distally of the stamen zone with the head facing the anthers downwards; pollen may adhere to the frontal part of the body, and the second and third pairs of legs may come into contact with receptive stigmas and thus transfer attached pollen grains (Pl. 1 Fig. 2);
- (iii) the insect is seated on the already wilted portion of the inflorescence below the stamen-bearing zone in a vertical position with the head in the upward direction; pollen may adhere to the frontal parts of the body but also to its under surface (Pl. 1 Fig. 3);
- (iv) the fly clings in a nearly horizontal position to one or more stamens in the lower part of the whorl of stamens; contamination of particularly the lower surface of the body with pollen is possible (Pl. 1 Fig. 4);
- (v) in the case of spikes in which the zone of male anthesis has almost shifted to the top: the insect sits on the tip of the inflorescence in a more or less horizontal position; pollen grains will become attached to mainly the frontal parts of the body, and deposition can take place as long as receptive stigmas are present (Pl. 1 Fig. 5).

More or less intermediate positions occur frequently, and during feeding the fly may shift its position.

The syrphids are repeatedly found on the stigma-bearing zone of the inflorescence, more particularly in the following situations:

- (a) the fly alights on this part and after a shorter or longer sojourn proceeds to the stamen-bearing zone; sometimes it stays for a while, usually cleaning and preening its body; (b) after feeding on the pollen the insect walks from the stamen-bearing zone towards the stigma-bearing part and usually stays there for some time preening its body; it sometimes returns to the male zone to resume pollen consumption, but may also fly away (Pl. 1 Fig. 6).

If the female phase of anthesis has not terminated, the legs or the ventral side of the body may get in touch with receptive stigmatic surfaces, which may result in pollen transfer. In the first situation described above (a) the chance of cross-pollination is greater than in the second (because in the latter case the pollen is likely to originate from the same spike).

#### SEM studies of the captured flies

After the presence of pollen grains on the bodies of flies captured immediately

after a visit to a *Plantago* inflorescence had been established by examination under a binocular dissecting microscope, a more detailed study was made by means of SEM microphotographs. For practical reasons only attention was paid to the ventral surface of the body (including the extremities). The study served a dual purpose: the pollen grains present could be identified more accurately, and the distribution of the pollen across the fly could be studied.

### Methods

The flies were captured when they were resting on vegetative parts of plants and never when they were sitting on inflorescences so as to avoid possible contamination with the large quantities of pollen shaken out of the anthers when one is handling the killing jar. For each fly a separate, clean jar was used to avoid indirect contaminations as much as possible. After a captured fly had become sufficiently desiccated it was mounted with its dorsal side on an object support by

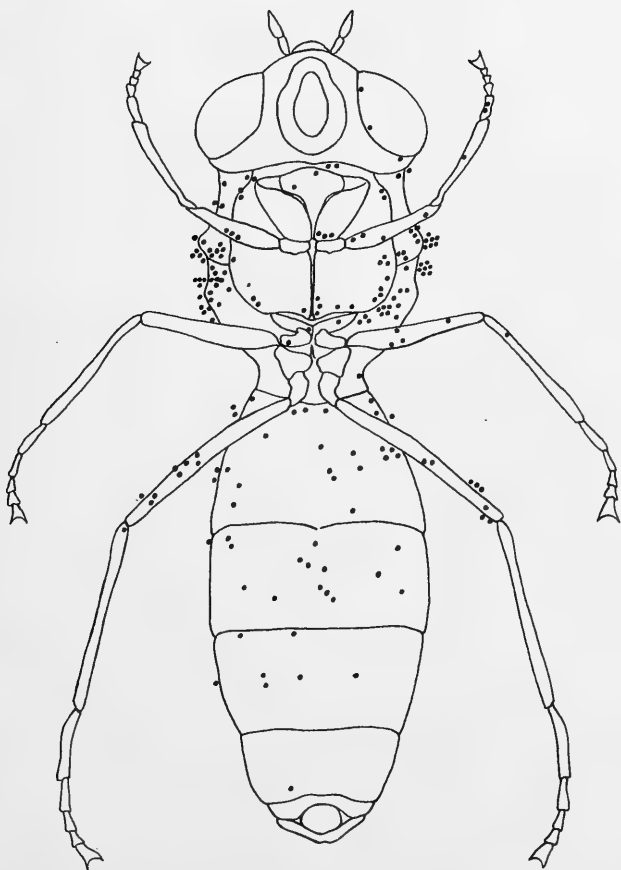


Fig. I. "Pollen map" of a syrphid fly (see text). The black dots represent pollen grains of *Plantago lanceolata* (dots situated outside the outline of the body represent pollen grains attached to setae protruding from the surface of the fly body)

means of silver cement and coated with gold in an Edwards (model E 12 E) vacuum-coating apparatus. The coated specimens were systematically scanned for adhering pollen grains at suitable magnifications in a Cambridge Mark II Stereoscan (acceleration potential 10 KV). A schematic outline drawing of a fly was used to map the localisation and the species of the identified pollen grains; for each specimen a so-called pollen map (an example of which is shown in Fig. 1) was made in this way. Special and characteristic situations were photographically recorded.

### Results

In all 32 syrphids were studied which belonged to all four species mentioned in the introduction. On all but one of these specimens the presence of pollen grains could be demonstrated. This pollen was almost exclusively of *Plantago lanceolata*; only in two cases a few gramineous grains were noted. The number of grains per fly varied a great deal: from a single one to a recorded maximum of 179 with a mean of 44. The localisation of the pollen on the ventral body surface was as follows: on the head only a few grains were observed, if any, and even around the mouth there were very few or none. The thorax carried the greatest number as a rule, especially in the pleural parts and on the hairs found in this part of the body. The abdomen bore fewer grains, mainly on the belly. Of the leg parts the femur carried the largest number of grains; between the three pairs of legs no important differences were found.

### Discussion

The scanning technique demonstrated conclusively that pollen grains of *Plantago lanceolata* adhere to the bodies of the syrphid flies. The relatively few number of specimens studied do not permit an accurate assessment of the distribution of the pollen on the bodies of the flies, but it seems as if the head does not carry many grains. The grains are sometimes found on the glabrous cuticle, but more often adhere to the dermal setae and do not always touch the cuticle. The attachment is almost certainly attributable to a cementing substance, whose presence (in small amounts) in *Plantago* was shown by Pohl (1930) and Knoll (1930) almost simultaneously. On SEM microphotographs (compare Plate 2) the pollen grains, when lying close together, are frequently connected by a mass forming a conspicuous meniscus. Also between a grain sticking to a hair and the support such a substance is present. Pollen grains pretreated with ethanol before SEM examination do not show this phenomenon, so that it appears to be highly probable that the connecting matter is hardened pollen "*Kitt*" covered by a gold film. The almost complete absence of grass pollen on the flies is of special interest. Conceivably, its relatively great rarity has something to do with the incidental nature of visits to species of Gramineae for feeding purposes. It is also known that the surface of gramineous pollen grains is only very thinly covered with *Pollenkitt*, although the absolute quantity may vary appreciably from species to species (Pohl, 1930); this small amount of cementing substance may account for the poor sticking capacity of the grains (or for a short duration of their attachment during the flight

of the insect). One must also bear in mind that the handling of the flies during the capture and their subsequent preparation may rub off a number of grains from the fly body, so that the SEM images do not necessarily present the situation immediately before the insects were caught: grass pollen may be rubbed off more easily than the plantain pollen.

### Concluding remarks

Field observations of syrphid flies regularly feeding on *Plantago lanceolata* indicate that these insects may easily become contaminated with pollen. More casual visits to the inflorescences of grasses with easily accessible anthers may also result in the adherence of pollen to the body.

The efficiency of an insect as a pollinator is largely dependent on the constancy of its habits and its patterns of behaviour. If it frequently moves from one plant in anthesis to the inflorescence of a different individual of the same plant species the chance of transfer of specific pollen is appreciable. However, the efficacy of zoophilous pollination is also determined by the amount of pollen carried by the animal vector on its body, which amount differs from plant species to plant species owing to the varying quantities of pollen and to the presence or absence of other aids for the adherence of the grains to the insect body (such as a rough or spinulose ectexine). As far as can be deduced from the available data, grass pollen is less effectively transferred than plantain pollen, which may be interpreted as a greater reliance upon pollination by syrphid flies of *Plantago lanceolata* as compared to the grasses, at least in the area under investigation. This needs verification, and this relation should also be studied in other habitats.

The different amounts of plantain and grass pollen recorded on captured flies support the idea of a greater dependence of *Plantago lanceolata* on the flies in its pollination strategy. The repeated visits of syrphids to different individuals in stands of plantain render an efficacious pollen transfer highly probable. It also enabled the demonstration of the transfer of pollen from one plant to another to be dealt with in the next chapter.

## II. EXPERIMENTS WITH STAINED POLLEN OF *Pantago lanceolata* L.

After the transfer of pollen of *Plantago lanceolata* by certain syrphid flies had been shown to be highly probable (see the first chapter), experiments were carried out to demonstrate the actual translocation of pollen grains from one plant to another by means of pollen marked by artificial staining. It has already conclusively been shown by means of SEM microphotographs that pollen grains adhere to various parts of the fly body, but although there were cogent indications of the role of the insects as effective pollen vectors, there remained some uncertainty whether a deposition by the flies of pollen grains on the receptive stigmatic surfaces of a flower in the female stage of anthesis actually takes place. By using artificially coloured grains partly replacing the normal pollen the identification of pollen grains deposited on other inflorescences was made possible, so that the displacement of this pollen could be traced. In addition, it was

hoped that from such experiments certain ideas concerning the efficacy of a biotic pollen transfer under field conditions could be gleaned.

### The marking of pollen by staining

Some preliminary tests had shown that pollen of *Plantago lanceolata* can readily be dyed by means of aqueous solutions of biological stains such as 0.5 % Methylene Blue and 0.5 % Neutral Red. Attempts to dye pollen grains still enclosed in the ripe anthers by spraying the inflorescences with such staining solutions were not very successful. Only a relatively small amount of pollen present near the slit of dehiscence appeared to have absorbed the dye, but the solution did not penetrate far enough. The anther wall may be more or less water-repellent. It was decided to use a technique in which pollen collected in the field was dyed in the laboratory as follows.

Pollen from spikes bearing numerous stamens in anthesis was harvested by beating the spikes over a metal tin. To obtain a quantity sufficient for subsequent processing at least 20-30 inflorescences must be shaken out. A small quantity of the collected pollen is poured on a disc of filter paper covering the bottom of a petri dish and spread out evenly by means of a fine paint brush. The dish is sprayed with the dye solution from a flower sprayer until the filter paper has assumed the colour of the solution. The (open) dish is left to dry in a suitable place at room temperature, which takes 2-3 hrs. To assess the condition of the grains the dish is placed under a dissecting microscope and the grains are touched with a fine preparation needle: if they are loose and can be easily shifted (or even jump away) the pollen is sufficiently desiccated. It is subsequently transferred to a glass tube with a brush and can be kept for some time until needed.

Pollen treated in this way was examined for some properties required for the purpose of the present investigation:

(i) Stained and normal (= untreated) pollen grains observed under a microscope at magnifications of 100—200 diam. appear to be always clearly distinguishable from one another;

(ii) When marked pollen was poured on to receptive stigmatic surfaces and the stigmas were subsequently examined under a dissecting microscope, such treated pollen grains appeared to adhere firmly to the stigmatic papillae and were clearly distinguishable in situ from untreated grains;

(iii) When living syrphid flies of the taxa studied (*Melanostoma*, etc., see the first chapter of this paper) were placed in a tube with dyed pollen, left in the tube for several minutes, and narcotised for examination under the microscope at a magnification of about 40 diam., they proved to carry a substantial amount of pollen on their bodies; the localisation of the pollen grains was very much the same as in the case of contamination with untreated pollen.

The treated grains apparently do not differ appreciably from undyed ones in some properties essential for their transfer by flies. To remove possible remaining doubts, the power of adherence of untreated and of dyed pollen was tested by locking up syrphids in a petri dish containing a small amount of a mixture of untreated and dyed grains in a known quantitative relation. After a brief sojourn



the flies were narcotised and their bodies were examined for adhering pollen. From counts of the two kinds of grains for each fly (42 specimens) the relation between untreated/dyed pollen was estimated.

The result was as follows:

mean ratio untreated/dyed pollen in the mixture:  $4.41 \pm 0.12$  [mean ratio untreated/dyed pollen on the fly bodies:  $5.18 \pm 0.54$ ].

### Experiments in the field: methods

For the experimental set-up the following reasoning was followed (see also the situation sketch, Fig. 2): When of two groups of flowering plants in a sufficiently

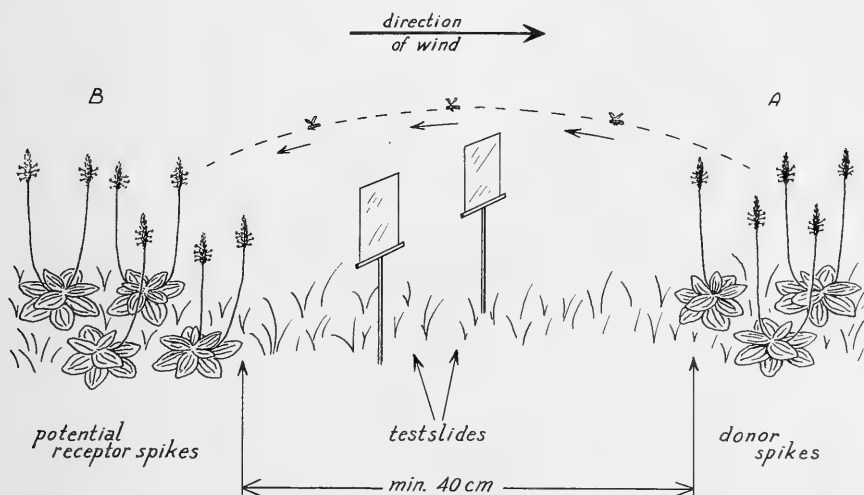


Fig. 2. Situation sketch of a field experiment (explanation in text). For the sake of clarity the rosette of leaves is drawn as if they are addressed to the ground (as in *Plantago major* and *P. media*)

dense stand of *Plantago lanceolata* one (A) is used as the donor group by applying dyed pollen to the spikes in the manner to be described below, and the other group (B) is left undisturbed, a syrphid fly visiting one or several donor spikes is likely to become covered with pollen including a number of treated grains. If it subsequently alights on untreated spikes there is a distinct possibility of dyed pollen becoming deposited on the stigmas of these spikes, which can be established by examining such spikes under a dissecting microscope (Pl. 3 Fig. B).

During the practical execution of the experiments the possible transfer of wind-borne pollen had to be taken into account. The relative position of the group of donor spikes was chosen in such a way that it always remained below the wind in respect of the untreated spikes present in the neighbourhood. A very favourable circumstance is that the syrphids tend to fly against the direction of the air current over the site, in the figure from group A towards group B. It goes without saying that this increases the efficacy and the reliability of the experiment.

In order to establish if nevertheless an undesired pollen transport of stained

pollen took place, test slides were placed between the two groups which were coated with egg-white glycerol on the one side to catch air-borne pollen grains; these slides were placed at a height a little below the average height of the donor spikes, with the smeared side facing the latter. The distance between the groups of donor plants and receptor plants must not be too short (at least 40 cm) so as to avoid the risk of an undesired pollen transfer by direct contact between plants or by air turbulence. The area chosen for such experiments was always limited enough to be easily surveyable from one observation post and thus to permit the reliable recording of visits to receptor spikes by flies coming from donor spikes by following the flight of the latter.

After some trials a method was worked out to bring about a contamination of flies with dyed pollen which agrees to all intents and purposes with the mode of contamination with untreated pollen during a normal visit to an inflorescence. Dyed pollen is placed on a flowering spike as follows: A sufficient quantity of dyed pollen is put in a glass tube of about 10 cm long and 1.5–2 cm in diam. By shaking and tapping the tube whilst turning it about its longitudinal axis in a nearly horizontal position the pollen is evenly distributed over the inner wall. Such a tube is placed over a spike in male anthesis with a well-developed zone of stamens, the inflorescence during this and the subsequent operations being held in a horizontal position by bending its stalk carefully. By pushing the spike to and fro and, if necessary, by turning the tube a bit, some of the dyed pollen is rubbed off and sticks mainly to the anthers (but also to other parts of the inflorescence such as the stigmatic zone). The spikes must be dry; damp ones moisten the inside of the tube too much so that the pollen sticks too firmly to the tube and becomes useless. Such a treatment of the inflorescences does not deter flies from visiting them normally, even if the whorl of stamens has assumed a somewhat unnatural colour. The dyed pollen grains are as readily consumed as untreated ones; in a number of cases a marked bluish-green discolouration of the abdomen of a fly was observed after the animal had been feeding copiously on spikes treated with stained pollen. It may, therefore be taken for granted that the deposition of marked pollen grains on a spike does not affect the normal behavioural pattern of the flies in the least. The added pollen is also dispersed in a normal way by air currents as could be deduced from the gradual disappearance of the greyish discolouration, after some time, of a spike treated with pollen dyed blue, even if no insect visits took place. Examination of flies captured after they had visited a donor spike revealed the presence of coloured pollen grains on the fly body (Pl. 3 Fig. A).

### Experiments in the field: results

Altogether 22 experiments were carried out, the duration of each single experiment being 60 to 150 minutes. The number of (treated) donor spikes was 3–6 and the receptor spikes usually numbered 3–4. Of about 90 spikes which were gathered in the field and might carry stained pollen grains ultimately only 67 could be used for the records, because some mishaps occurred which rendered them unusable (some became soaked with water, etc.).

The following qualifications need some explanation.

**Fresh stigmas:** stigmas with a shiny, somewhat vitreously white appearance; the distal parts may be suffused with brown.

**Old stigmas:** stigmas which have mostly or completely turned brown and have often become desiccated.

The duration of the receptive phase of the stigmas is not exactly known, but nevertheless the distinction made above, based on a different appearance, corresponds most probably with the receptive phase and the phase of post-anthesis of the stigmas.

After the experiments were concluded, a publication by Zeisler (1938) came to our notice in which a simple method is described to assess the degree of 'maturation' (receptiveness) of the stigmas by a chemical reaction (with  $H_2O_2$ ). If this test is applicable to *Plantago* stigmas, some relevant additional information may thus be acquired.

**Whole spike:** includes bracts, perianth members, stigmas, and a zone of stamens.

**Stigma ratio (s.r.):** 
$$\frac{\text{number of stigmas with stained pollen grains}}{\text{total number of stigmas}}$$

**Control with test slides:** The pollen counts were made of a rectangular area of 10 mm by 20 mm in the middle of the slide at a magnification of 100–200 diam. Not in a single instance stained pollen was recorded, but a few undyed grains were usually present; the latter may have been deposited by air turbulence or

Table 1. Presence or absence of dyed pollen on spikes of *Plantago lanceolata* L.

	Marked pollen present in	Marked pollen absent in
On fresh stigmas	43 spikes	24 spikes
On fresh and/or old stigmas	48 spikes	19 spikes
On whole spikes	50 spikes	17 spikes

convection currents, or as fall out of the local pollen rain from somewhat higher levels. In a number of cases test slides were also placed in a downwind position and these almost invariably had caught large quantities of both stained and unstained pollen.

The (67) receptor spikes were examined for the presence of marked pollen grains and the results are as follows (Table 1).

Table 2. Distribution of dyed grains over spikes of *Plantago lanceolata* L.

Number of dyed grains	Number present		
	On fresh stigmas	On old stigmas	On whole spike
(0)	(24)	(19)	(17)
1-10	25	15	11
11-20	8	14	11
21-50	7	14	18
51-100	2	2	5
more than 100	1	3	5
	—	—	—
	43	48	50

The following survey shows the number of individual grains in the cases in which dyed pollen had been transferred (Table 2). In the accompanying tabel (Tabel 3) the stigma ratio of 41 spikes with transferred dyed pollen grains, and the

Table 3. Stigma ratio (s.r.) and number of grains on 41 spikes with transferred dyed pollen grains

s.r.	number of grains	s.r.	number of grains	s.r.	number of grains
3/9	- 8	10/10	- 136	1/1	- 3
1/10	- 4	2/2	- 19	6/10	- 36
6/7	- 63	7/9	- 47	4/11	- 20
1/12	- 3	3/6	- 19	13/36	- 32
12/17	- 98	4/8	- 26	2/6	- 2
8/10	- 47	5/13	- 12	6/9	- 26
1/29	- 2	1/17	- 2	4/11	- 4
2/4	- 9	1/23	- 4	2/26	- 9
4/8	- 31	1/21	- 12	1/8	- 1
2/11	- 7	2/4	- 3	1/22	- 1
5/17	- 10	4/14	- 14	3/3	- 19
2/3	- 7	1/11	- 2	3/4	- 6
2/7	- 5	2/14	- 5	3/9	- 10
4/7	- 9	3/21	- 13		

number of grains on the stigmas is shown. Of two of the 43 spikes with stained pollen grains the number of fresh stigmas was inadvertently not counted.

### Discussion

The examination of the test slides indicates that an abiotic transportation of pollen against the direction of the wind is negligible. The conclusion that can be drawn from the results of the first survey (Table 1) is that syrphid flies are instrumental in the transfer of pollen from one spike to another and can do this repeatedly. The absence of marked pollen grains on potential receptors can have several reasons, the most important being:

(a) that the spikes were not visited by flies, or

(b) that the spikes were visited, but by flies that did not carry stained pollen grains.

One can only speak of an effective pollination if pollen is deposited on fresh (and presumably receptive) stigmas. This was the case in 20 experiments and in 64% of the total number of spikes examined, so that the general conclusion remains valid. One of the surveys (Table 2) gives a good idea of the quantities of marked pollen grains transferred by the animal pollen vector, but the results do not require a special discussion.

From the viewpoint of efficacy of pollen transfer the number of stigmas on which dyed pollen had been deposited is important. Table 3 shows that there are appreciable differences in this respect, both in stigma ratio and in the number of stained grains. This is to be expected if one considers that a number of mutually independent factors is involved in the pollen transfer to the stigmas, viz.,

(a) the total number of visits to a spike,

- (b) the duration of these visits,
- (c) the mode of landing, behaviour and/or displacement of the pollen vector,
- (d) the amount and the location of the pollen on the body of the visitor, and
- (e) the number and the length of the stigmas on the particular spike.

The first two factors could be quantified by the registration of the visits, but there was no correlation with the quantity of deposited marked pollen. Matters were complicated by the uncertainty in many cases whether a visitor was indeed a carrier of dyed pollen. The dyed grains were especially deposited on the tips of the stigmas as may be expected because these protruding parts are the most likely to come in touch with the insect body. It is also noteworthy that stained grains were localised on the stigmas in groups.

Another survey (Table 4) demonstrated that of all pollen-bearing stigmas only

Table 4. Distribution of stained pollen grains over the stigmas

---

36 stigmas (24.3%) with 1 grain
24 stigmas (16.2%) with 2 grains
24 stigmas (16.2%) with 3 grains
64 stigmas (43.3%) with 4 or more grains

---

24% had caught a single dyed grain, whereas in 76% of the cases two or more grains were present. Since the gynoeceum contains 2(-3) ovules the theoretical chance of efficacious fertilization is rather great.

The experiments described in the previous chapter render it highly probable that pollen treated with stains has practically the same properties as untreated pollen at least as far as its power of adhesion to the insect body and of its successful translocation is concerned. It is, in our opinion, not necessary to put its equivalence with regard to adhesion to the stigmatic surface to the test: the sticky stigmas readily retain all sorts of particles (some of which are larger than the pollen grains) and their capacity to capture pollen grains by their adhesive properties certainly exceeds the affinity of the pollen grains to the surface of the insect body. Various considerations render the same chances of being transferred by biotic agencies. Considering that untreated pollen seems to adhere slightly better to the insect body, the transfer of untreated pollen by flies can be accepted beyond reasonable doubt, even if the transfer of untreated grains from a donor spike to a receptor spike could not be directly demonstrated: untreated pollen found on receptor spikes may have been deposited by a fly coming from a donor spike but just as well from various other sources outside the experimental area.

One must bear in mind that the duration of the experiments was usually shorter than the time-span of the daily visiting period (although it always included the phase of optimum activity of the flies), so that an — albeit relatively small—part of the potential pollen transfer was not recorded. This only means that the rate of biotic pollen transfer is undoubtedly slightly higher than it appeared to be under our experimental conditions. The fact that the flies often move about on the same spike (and preen themselves) favours the incidence of geitonogamy, and so does their habit of frequently moving towards inflorescences in the immediate neighbourhood (which may well belong to the same individual of *Plantago*

*lanceolata*), but our experiments have shown that effective cross-pollinations are by no means rare.

As far as the relative importance of efficiency of the biotic and the anemophilous form of pollen transfer is concerned, the present experiments do not permit a clear verdict. A specially adapted method (by means of fertilisation experiments?) would have to be worked out for the purpose.

An ecologically interesting and relevant circumstance is that the syrphid flies of the *Platycheirus-Melanostoma* group as a rule visit the *Plantago* inflorescences during the first hours of the morning (see the first chapter). At that time of the day the wind is often hardly noticeable or at least very weak, so that presumably the relative share of the biotic pollen transfer in respect of that by air currents will be greater than later during the day. Local differences in the relative rates of the two types of pollination associated with different environmental conditions and habitat variation (such as landscape and vegetation type and microclimatological differences) cannot be precluded. The question in how far these variations may be correlated with, or reflected in, modifications of the inflorescence is of interest. Delpino (1870, cited and discussed in Müller, 1873) thought he could recognise forms with differences in structural adaptation, which was accepted with some diffidence by the latter author.

One should never lose sight of the fact that a biotic transfer of pollen of *Plantago lanceolata* as described in the present paper can only take place where this plantain and the potential pollinators occur sympatrically, which need not always be the case. Field observations and experiments in other areas are indicated, and it will be necessary to extend the investigation by comparing the anthecological syndromes of other species of *Plantago* with the situation in *P. lanceolata*.

The technique for the dying of pollen for purposes of specific identification after a possible transfer can probably be improved and extended to be used effectively for the study of other cases in which different taxa and plants and other (potential) pollen vectors are involved. Coldwell (1951) has developed a useful method to study the dispersal pattern of air-borne pollen (of different species of conifers) by using pollen labelled with radioactive substances (isotopes). This technique is rather laborious, however, and other workers who have attempted to apply this method have not been successful (B. J. D. Meeuse, priv. comm.). The use of artificially stained pollen permits a more or less small-scale approach to various anthecological problems, more particularly in border-line cases between entomophily and anemophily.

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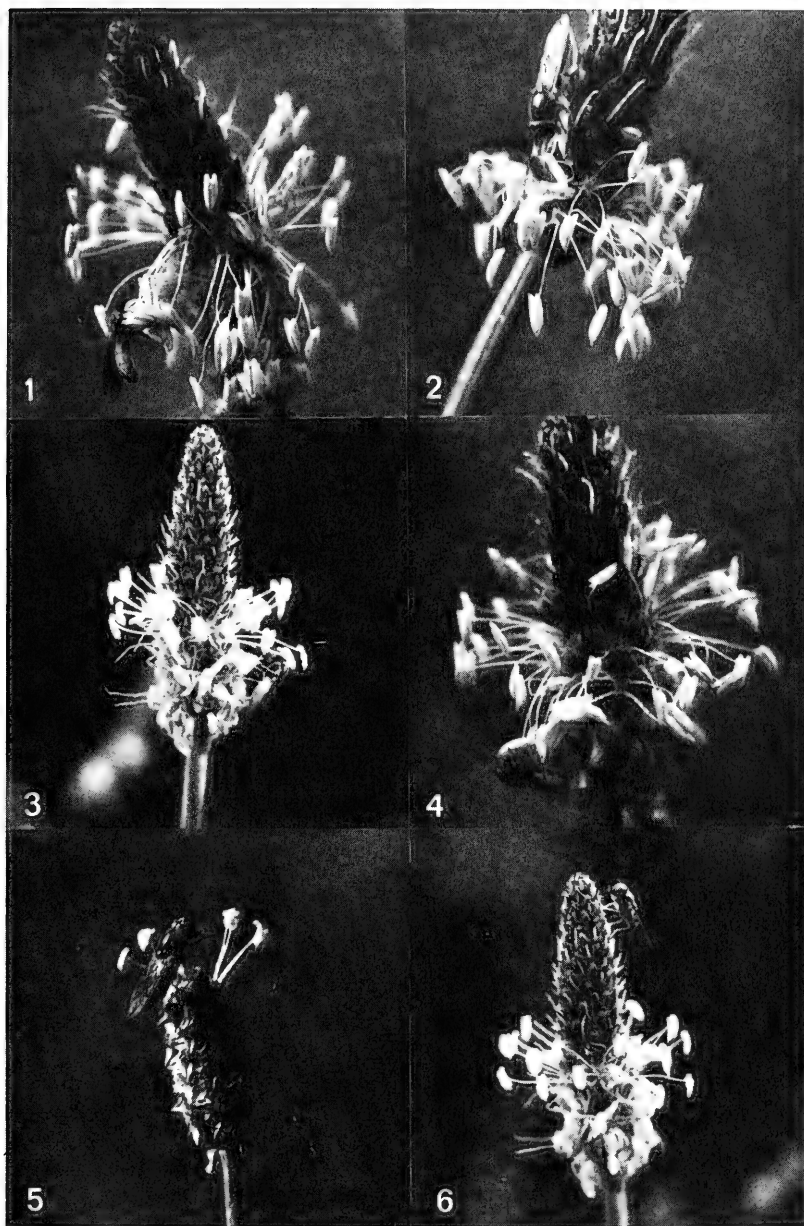
The permission granted by the „Vereniging tot Behoud van Natuurmonumenten in Nederland” to do field work in the Naardermeer nature sanctuary deserves grateful memorisation.

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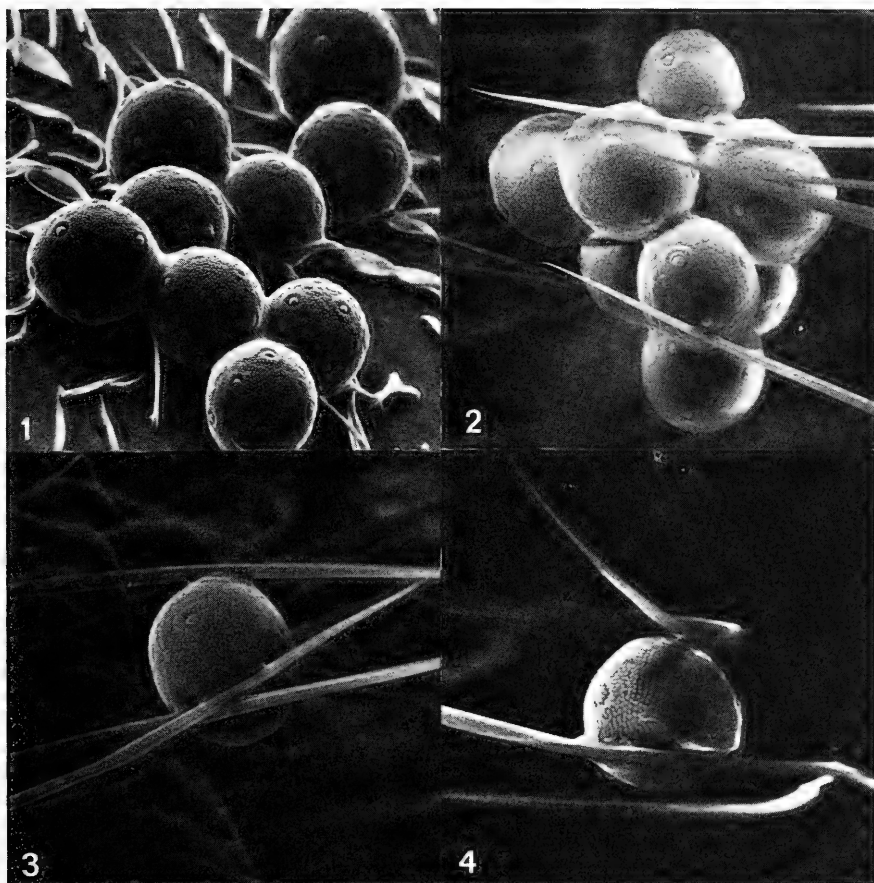






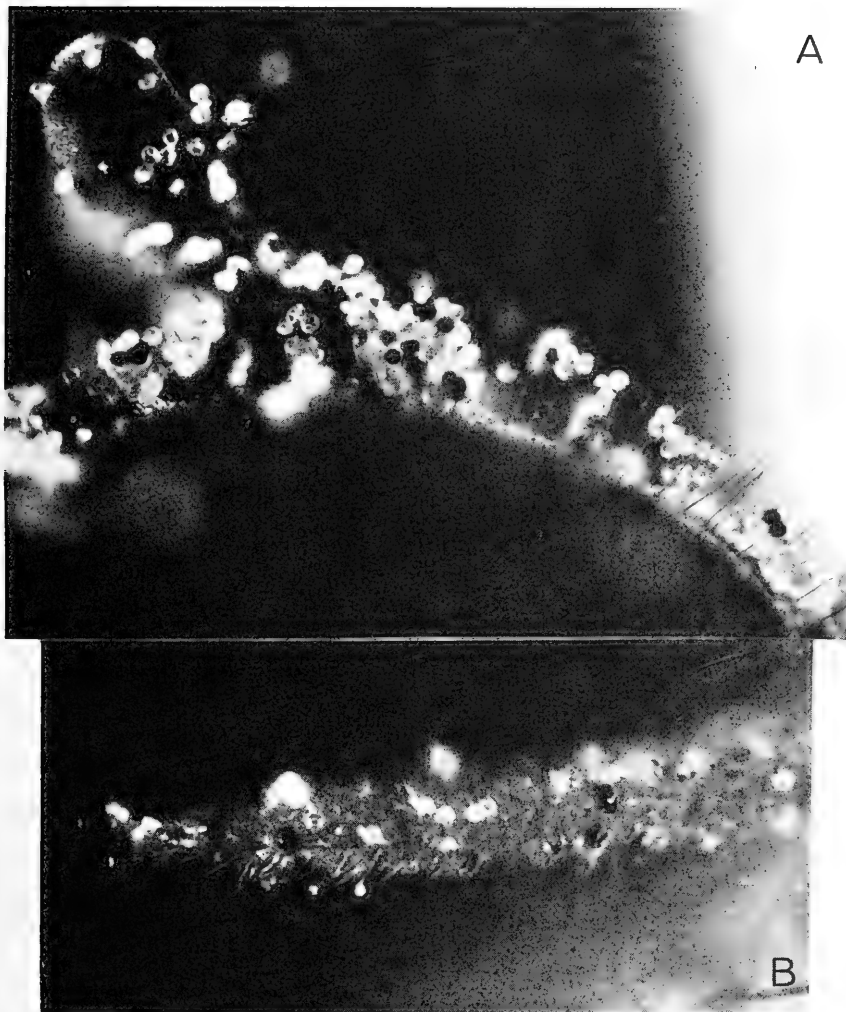
Different positions of syrphid flies on inflorescences of *Plantago lanceolata* (explanation in text)





SEM microphotographs of pollen grains of *Plantago lanceolata* on the bodies of syrphid flies.  
1, X 600; 2, X 720; 3, X 900; 4, X 900





A. Part of the head of a syrphid fly to which normal (light coloured) and stained (dark coloured) pollen grains are attached, X 50. B. Stigma of an inflorescence of *Plantago lanceolata* collected after a visit by a fly, showing the presence of untreated (light coloured) and stained (dark coloured) pollen grains, X 50









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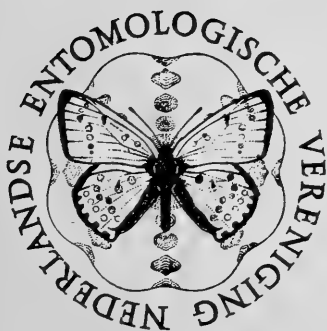
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C. VAN ACHTERBERG. — A preliminary key to the subfamilies of the Braconidae (Hymenoptera), p. 33—78, fig. 1—123.



# A PRELIMINARY KEY TO THE SUBFAMILIES OF THE BRACONIDAE (HYMENOPTERA)

by

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*Rijksmuseum van Natuurlijke Historie, Leiden*

With 123 figures

## Abstract

A preliminary key to the subfamilies of the Braconidae is given. The subfamilies are redefined in the key and in a short description. Especially the apomorphous characters, which may be used to define the subfamilies, are discussed.

## INTRODUCTION

The family Braconidae can be separated from its sister-group, the Ichneumonidae, by at least two synapomorphous characters. The most important is the rigidly joined 2nd and 3rd tergites of the metasoma and, secondly, the absence of the second recurrent vein. The rigid plate formed by the 2nd and 3rd tergites may be weakly sclerotized (as in the Aphidiinae) or may be completely fused, e.g., in the Hybrizontinae and Acaeliinae.

The first worker, who tried to give a classification of higher groups was Wesmael (1835), whose classification concerned only the Palaearctic region. The Braconidae were divided into two divisions by Wesmael (p. 11): the "braconides endodontes" and the "braconides exodontes". The latter group is what is now called the Alysiinae. The "endodont"-Braconidae were divided into four subdivisions (p. 14): (1) the "polymorphes", (2) the "cryptogastres", (3) the "areolaires", and (4) the "cyclostomes". The "polymorphes" contain the Aphidiinae, Euphorinae, Helconinae, Ichneutinae and Opiinae. The "cryptogastres" are an aggregate of Cheloninae and convergent groups, belonging to the Helconinae and Meteorideinae. The "areolaires" embrace the convergent groups Microgasterinae, Acaeliinae, Orgilinae and Agathidinae. Finally the "cyclostomes" contains the Doryctinae, Rogadinae and Braconinae, as treated in the present paper. The first reviser of this system was Foerster (1862), who gave a very elaborate sub-division and defined 26 "subfamilies", to which he added the suffix "-oidae". The following systems were based more or less on the Foerster-system, but several "subfamilies" were given tribal rank in one large subfamily. E.g., the Braconoidae, Euspathioidae, Hecaboloidae, Doryctoidae, Hormioidae, Rogadoidae and Rhyssaloidae became in Fahringer (1925) the tribes Braconini, Spathiini, Hecabolini, Doryctini, Hormiini, Rhogadini, Exothecini and Pambolini in one subfamily Braconinae, in effect the old "cyclostomes" of Wesmael. The "Sigalphoidae" became a part of the Helconinae, while the "Chelonoidae" are the

present Cheloninae and Meteorideinae. The "Microgasteroidae" contain the Microgasterinae and Acaeliinae, and the Agathidinae were divided by Foerster in the "Agathidoidae" and the "Eumicrodoidae", while the last mentioned also contains the Orgilinae p.p. The "Pachylommatoidae" and "Aphidioidae" are called Hybrizontinae and Aphidiinae, respectively, in the present paper. The "Euphoroidae" and "Perilitoidae" form the Euphorinae, from which quite recently *Zemiotes* Foerster was excluded and added to the Zelinae (Mason, 1973). The "Brachistoidae" of Foerster are of composite nature, they belong partly to the Helconinae and partly to the Zelinae (as defined in the present paper). The "Liophronoidae", together with *Pygostolus* Haliday from the "Blacoidae", form the tribe Centistini in the Euphorinae. The remainder of the "Blacoidae" belongs to the Helconinae. The "Ichneutoidae" and "Helconoidae" became the Ichneutinae and Helconinae p.p., respectively. Foerster's "Macrocentroidae" contain the Macrocentrinae and *Zele* Curtis of the Zelinae; this grouping is still widely used, e.g., by Eady & Clark (1964) and Čapek (1970). The "Diospiloidae" belong to the Helconinae and Orgilinae. Except for *Gnaptodon* Haliday (which is included in the Rogadinae), his "Opioidae" are fully comparable with the Opiinae. Ultimately his "Alysioidae" and "Dacnusoidea" are united by Griffiths (1964: 831) in the subfamily Alysiinae; this was confirmed through the study of the larvae by Čapek (1970: 861).

The system used by Marshall (1885: 9) is essentially that of Wesmael, but he added as a sixth division the "Flexiliventes" for the Aphidiinae, because of their flexible and weakly sclerotized metasoma. In 1891 he added as a seventh division the "Pachylommatidae", now called Hybrizontinae. These mainly large groups were subdivided according to the system of Foerster with some modifications, but also resulting in 26 "subfamilies" (for which Marshall used the suffix "-ides") for the Palearctic region.

The key by Ashmead (1900: 111) to the subfamilies of the Braconidae is the first general key, intended to be used in more than one region. Ashmead separated the Alysiinae as a family Alysiidae, while the remaining genera were divided among 17 subfamilies. His division and interpretation of the genera was often incorrect, because he used a modification of the Foerster system without examining the types of many genera.

The second and latest general key to the subfamilies, which was used more extensively, is the key published by Szépligeti in 1904. It divides the Braconidae into 31 subfamilies, one of which (the Lysiognathinae) belongs in the Ichneumonidae. From the remaining 30 subfamilies the following are removed and reduced to lower rank in the subfamilies mentioned in parentheses: Cenocoelininae (Helconinae), Gnathobraconinae (Rogadinae), Aphrastobraconinae (Braconinae); Exothecinae (Rogadinae), Spathiinae (Doryctinae), Hecabolinae (Doryctinae), Pambolinae (Rogadinae), Hormiinae (Rogadinae), Sigalphinae (Helconinae), Calyptinae (Helconinae), Liophroninae (Euphorinae), Blacinae (Helconinae), Cardiochilinae (Microgasterinae), Diospilinae (Helconinae), Meteorinae (Euphorinae) and Dacnusoidea (Alysiinae). The remainder, 14 subfamilies, are augmented to 22 in the present paper, because of three newly described subfamilies (Ypsistocerinae Cushman, 1923; Telengainae Tobias, 1962; Mesostoinae Van Achter-

berg, 1975) and a rearrangement of five groups according to Čapek (1970 and 1973) and Tobias (1967). These five subfamilies are the Acaeliinae and Zelinae (according to Tobias), the Orgilinae, Meteorideinae and Neoneurinae (modified after Čapek).

The two subfamilies erected by Fahringer (1936: 586) in his fairly general (but rather confusing) key are not accepted in the present paper. His *Aneurobraconinae* (containing the genus *Aneurobracon* Brues) is provisionally treated in this paper as a tribe of the Agathidinae, while the *Pseudodicrogeniinae* (containing only the genus *Pseudodicrogenium* Fahringer) is included as a tribe in the Braconinae. The morphology of both types examined clearly justify this transfer (Fig. 120—122).

After Szépligeti, several others have given subfamily-keys for the Palaearctic region (e.g., Fahringer, 1925; Tobias, 1971), while Marsh (1963: 522) gave a key for the Nearctic region. This key was disregarded in his later key to the Nearctic genera (1971: 841), because "there is some disagreement as to the limits of the various subfamilies in the Braconidae, . . .".

For the terminology used, see Van Achterberg, 1976.

#### DISCUSSION

The main reason for the confusion in the systematics of the Braconidae is formed by the many convergent evolutionary trends, occurring in this group. Some of the most important trends are the following:

1. The reduction of the veins of the wing, e.g., the Blacini in the Helconinae versus the Centistini in the Euphorinae.

2. The forming of rows of setae, usually one row per tergite. In this respect I disagree with Griffiths (1964: 842), who stated that "the arrangement of hairs in single rows on the gastral segments, being found in almost all other Alysiinae and many other Braconidae is beyond doubt plesiomorph". I am convinced that the opposite is true: many species with many plesiomorphous character-states have the tergites evenly setose. Still more convincing is the fact that most Ichneumonidae (the sister-group, in most aspects clearly less evolved) have the metasomal tergites evenly setose.

3. The formation of a carapace, formed by the three basal tergites of the metasoma, e.g., in the Helconinae (Brachistini), Cheloninae, Microgasterinae (*Fornicia* Brullé), and Rogadinae (Tobias & Dudarenko, 1974).

4. The ovipositor becomes shorter, sometimes more or less curved, and its sheaths become often wider.

5. The reduction of the segments of the palpi; the plesiomorphous condition of the maxillary and labial palp is 6 and 4 segments, respectively. Lower numbers occur in e.g., the Braconinae, Alysiinae, Helconinae, Neoneurinae and Hybri-zontinae.

6. The selection of hosts other than Coleoptera larvae, especially Lepidoptera and Diptera.

7. The development of endoparasitism.

8. The parasitism of adult insects by the Neoneurinae, Aphidiinae and Euphorinae.

9. The reduction of the number of antennal segments occurs in almost all groups.

10. The development of a petiolus at the basis of the first metasomal tergite: e.g., Doryctinae (Spathiini), Euphorinae (Meteorini) and Zelinae (Zemiotini).

11. The forming of a hypoclypeal depression and a more or less concave clypeus: e.g., Braconinae, Opiinae, and Euphorinae (Cosmophorini).

12. The twisting of the mandible: e.g., Macrocentrinae, Braconinae and, very extremely, in the Alysiinae.

13. The formation of a dorsope and/or a laterope, while often also the dorsal carinae become more developed, until beyond the middle of the first tergite: e.g., Helconinae, Rogadinae, Alysiinae and Euphorinae.

14. The spiracle of the first metasomal tergite becomes situated near the middle of the tergite: e.g., Euphorinae and Zelinae (Zemiotini).

15. The radial cell becomes short and/or narrow, a tendency occurring in almost all subfamilies.

16. The first metasomal tergite becomes depressed, especially laterally: e.g., Mesostoinae, Braconinae, Microgasterinae, Acaeliinae and the tribe Proteropini of the Ichneutinae.

17. The convergent development of an "ophionoid facies" (Gauld & Huddleston, 1976) an adaption for nocturnal activity, occurring in the Zelinae, Euphorinae, Macrocentrinae and Rogadinae.

18. The mandibles of the larvae become slender and toothless: e.g., Euphorinae, Neoneurinae, Aphidiinae, Alysiinae, Opiinae, Microgasterinae p.p., and Rogadinae p.p.

19. The reduction of the cephalic structures of the larvae, especially of the hypostoma: e.g., Euphorinae, Orgilinae, Helconinae (Blacini & Brachistini), Neoneurinae, Ichneutinae (Muesebeckiini), Opiinae, and Doryctinae.

20. The labial and stipital sclerites of the larvae become long and slender: e.g., Euphorinae, Helconinae, Zelinae, and Opiinae.

Mainly owing to the research by Čapek upon the cephalic structures of the final instar larvae, I have tried to construct a key to the subfamilies proposed by Čapek and Tobias. Some changes seem inevitable to me, e.g., the fusion of the subfamilies Rogadinae and Exothecinae. There are too many genera in these groups, that connect the groups in more than one character. The mummification of caterpillars by *Rogas* and closely allied genera is not sufficient (however peculiar it may be) to separate them as a subfamily. The Centistinae of Čapek (1970) are included in the Euphorinae, according to Čapek (1973). The Adeliini s.l., a tribe of the Microgasterinae in Čapek (1970), are redefined and partly maintained as the tribus Miracini in the Microgasterinae; the other part is treated as a separate subfamily, the Acaeliinae, according to Tobias (1967 and 1971, who used the name Adeliinae). The Orgilinae (the tribe Orgilini of the Agathidinae in Čapek, 1970) and the Braconinae (the tribe Braconini of the Braconinae in Čapek, l.c.) are treated as separate subfamilies. The three other tribes (Exothecini, Hormiini and Pambolini) of the Braconinae in Čapek are included in the Rogadinae. The Spathiinae of Čapek (1970) is at most a tribe of the Doryctinae, as pointed out by Čapek (1973: 267).

More problematic is the position of the genera *Zelee* (and *Zemiotes*), *Charmon* (= *Eubadizon* of Čapek), *Acampsis* and *Sigalphus*. Čapek (1970) included *Zelee* and *Macrocentrus* in his Macrocentrinae following, for example, Nixon (1938) and Eady & Clark (1964). But Watanabe (1969: 319) considered the most adequate location to be in a tribe Zelini of the subfamily Helconinae; also Čapek (1973) gave them a tribal rank. The larvae are distinct from the larvae of the Helconinae: the labial sclerite is pentagonal, while it is transverse (Cenocoeliini) or longitudinal (height larger than width in other tribes) in the Helconinae; they are endoparasites of Lepidoptera, while Helconinae are almost exclusively endoparasites of Coleoptera; and the imagines of *Zelee* and its relatives have several synapomorphous characters in respect to the Helconinae as treated in the present paper. It is therefore that I follow Tobias (1967, 1971), who gave this group subfamily rank, and I also include *Charmon* and *Zemiotes*.

The adult morphology of *Charmon* (e.g. the genitalia of the male, cf. Fig. 36, 40 in Tobias, 1967), its biology (also endoparasites of Lepidoptera) and the regular shape of the emergence opening from the cocoon (irregular in the Orgilinae, its near relatives) indicate the relationship with *Zelee*. The cephalic structures of the final instar larvae of *Charmon* (Fig. 15 in Čapek, 1970) are different from *Zelee*, because of the absence of the hypostomal spur, but the slender shape of the hypostomal parts and of the stipital sclerite make a relationship with the Zelinae more likely than with the Orgilinae (cf. Fig. 16, 17 in Čapek, 1970) as treated in this paper.

Still more complicated is the placement of *Acampsis*, *Sigalphus* and *Meteoridea*. The larvae of *Acampsis* and *Sigalphus* have slender mandibles with a very wide base (Fig. 34, 35 in Čapek, 1970), unlike the basally slender mandibles of the Cheloninae (Fig. 36, l.c.). Čapek overlooked this difference, because he included them in the Cheloninae (1970: 871), even in his key to the larvae (1973: 261) where he mentioned as the key factor for the Cheloninae "... (mandibles) without or only with a small base". Thus owing to the shape of some cephalic structures of the larvae and because of many differences in the adult morphology (e.g., nervellus broken, postpectal carina absent), I agree with Tobias (1967: 659), who gave this group subfamily rank. Unfortunately Tobias (l.c.) used the name "Sigalphinae", a name for a long time (incorrectly) used for a group now included in the tribus Brachistini of the Helconinae. Čapek (1970: 871) erected the subfamily Meteorideinae for *Meteoridea*, because the biology of this genus is rather peculiar. It is (at least partly) comprised of gregarious endoparasites of Lepidoptera-larvae, which let pupate the host larva and thereafter the parasites spin their cocoons inside the host cocoon. The stout stipital sclerite, the very wide base of the mandible of the larvae with its apical half slender and toothed (cf. Fig. 12, 34, 35 in Čapek, l.c.), combined with similarities in the morphology of the adults (e.g., nervellus broken, rather short radial cell, first discoidal cell petiolate and ovipositor sheath wide) give some indications about its relationship with the "Sigalphinae" of Tobias. Of the characters mentioned at least the slender apical half of the mandibles of the larvae, the stout ovipositor sheath of the adults and the rather short radial cell are synapomorphous. Therefore I propose to unite the Meteorideinae of Čapek and the Sigalphinae of Tobias into the Meteorideinae s.l.

Table 1. Divisions of the Braconidae given by some authors compared with the division proposed in the present paper

Wesmael, 1835	Foerster, 1862	Ashmead, 1900	Szépligeti, 1904	Muesebeck & Walkley, 1951	present paper
---	---	---	---	---	Ypsistocerinae
"Cyclostomes"	Doryctoidae ( <i>Histeromerus</i> Wesmael included), Euspathioidae, and Hecaboloideae Rogadoideae, Braconioideae p.p., Hormioidae, and Rhyssaloideae Braconioideae p.p.	tribes Doryctini ( <i>Histeromerus</i> Wesmael included), and Hecabolini of the Rhogadinae and the tribe Spathiini of the Spathiinae	Doryctinae ( <i>Histeromerus</i> Wesmael included), and Spathiinae	Doryctinae ( <i>Histeromerus</i> Wesmael included), and Spathiinae	Doryctinae ( <i>Histeromerus</i> Wesmael excluded)
		tribes Exothecini, Rhyssalini, and Rhogadini in the Rhogadinae and the tribes Pambolini and Hormini of the Spathiinae	Rhogadinae, Hormiinae, Pambolini, Exothecinae, and Gnathobraconinae	Rogadinae	Rogadinae ( <i>Gnaptodon</i> Haliday included)
		Braconinae	Braconinae and Aphrastobraconinae	Braconinae	Braconinae ( <i>Histeromerus</i> Wesmael included)
		---	---	---	Telengainae
---	---	---	---	---	Mesostoinae
"Polymorphes" p.p.	Opioidae ( <i>Gnaptodon</i> Haliday included)	Opiinae ( <i>Gnaptodon</i> Haliday included)	Opiinae ( <i>Gnaptodon</i> Haliday included)	Opiinae ( <i>Gnaptodon</i> Haliday included)	Opiinae ( <i>Gnaptodon</i> Haliday excluded)
		the Subfamilies Alysiniinae and Dacnusiinae of the Alysiiidae	Alysiniinae and Dacnusiinae	Alysiniinae and Dacnusiinae	Alysiniinae
"Exodontes"	Alysioidae, and Dacnusoideae				
"Argéolaires" p.p.	Microgasteroideae p.p. Microgasteroideae p.p.	Microgasterinae p.p.	Microgasterinae p.p.	Microgasterinae p.p.	Acaceliinae
		Microgasterinae p.p. Agathinae p.p., Sigalphinae p.p., and Cardiochilinae	Microgasterinae p.p., Agathinae p.p., Sigalphinae p.p., and Cardiochilinae	Microgasterinae p.p., Agathinae p.p., Sigalphinae p.p., and Cardiochilinae	Microgasterinae ( <i>Paroligoneurus</i> Muesebeck excluded)



"Cryptogastres" p.p.	Chelonoidea p.p.	Cheloninae p.p.	Cheloninae p.p.	Cheloninae	Cheloninae
"Polymorphes" p.p.	Ichneutoidea	Ichneutinae	Ichneutinae	Ichneutinae	Ichneutinae ( <i>Paroligoneurus</i> Muesebeck included)
"Crypogastres" p.p.	Chelonoidea p.p.	Agathidinae p.p., and Cheloninae p.p.	Agathinae p.p., and Cheloninae p.p.	Helconinae p.p., and Cheloninae p.p.	Meteorideinae
"Aréolaires" p.p.	Agathidoidea, and Eumicrodoidea p.p.	Agathidinae p.p.	Agathinae p.p.	Agathidinae	Agathidinae
"Polymorphes" p.p.	Macrocentroidea p.p.	Macrocentrinae p.p.	Macrocentrinae p.p.	Macrocentrinae	Macrocentrinae
"Polymorphes" p.p., and "Cryptogastres"	Helconoidea, Brachistoidea p.p., Blacoidae p.p., Diospiloidae p.p., and Sigalphoidea	Helconinae, Blacinae p.p., Diospilinae p.p., Sigalphinae p.p., and Cheloninae p.p.	Helconinae, Cenocoelinae, Diospilinae p.p., Calyptinae p.p., Blacinae p.p., Sigalphinae, and Cheloninae p.p.	Helconinae p.p., and Blacinae p.p.	Helconinae
"Polymorphes" p.p.	Macrocentroidea p.p., Perilitoidea p.p., and Brachistoidea p.p.	Macrocentrinae p.p., Meteorinae p.p., Dacninae p.p., and Blacinae p.p.	Macrocentrinae p.p., Calyptinae p.p., and Meteorinae p.p.	Helconinae p.p., Blacinae p.p., and Euphorinae p.p.	Zelinae
"Aréolaires" p.p.	Diospiloidae p.p., and Eumicrodoidea p.p.	Macrocentrinae p.p., and Blacinae p.p.	Agathinae p.p., and Diospilinae p.p.	Blacinae p.p.	Orgilinae
"Polymorphes" p.p.	Perilitoidea p.p., Euphoroidae, Blacoidae p.p., and Liophronoidae	Euphorinae, Meteorinae p.p., Blacinae p.p.	Euphorinae, Meteorinae p.p., Blacinae p.p., and Liophroninae	Euphorinae p.p., and Cosmophorinae	Euphorinae
---	Microgasteroidea p.p.	Microgasterinae p.p.	Agathinae p.p.	Neoneurinae	Neoneurinae
{ "Polymorphes" p.p.	Aphidoidea	Aphidinae	Aphidinae	Aphidinae	Aphidinae
	Pachylommatoidae	Pachylommatinae	Pachylommatinae	Pachylommatinae	Hybrizontinae

The division of the Braconidae given by Wesmael (1835), Foerster (1862), Ashmead (1900), Szépligeti (1904), and Muesebeck & Walkley (1951) are compared with the division given in the present paper in Table 1.

#### KEY TO THE SUBFAMILIES OF THE BRACONIDAE S.L.

1. Mandible unidentate (Fig. 10); antenna inserted on the top of the head (Fig. 8, 9); ovipositor issuing near middle of metasoma (Fig. 8); whole body densely setose (Fig. 8); associated with termites ..... *Ypsistocerinae* (p. 44)
- Mandible with 2—7 teeth; antenna inserted below top of head, at height of the eyes (Fig. 5, 11, 25); ovipositor issuing near apex of metasoma (Fig. 11, 68, 72, 89, 95, 108, 109); body less setose; associated with other groups ..... 2
2. Mesoscutum protruding above pronotum (Fig. 11); epistomal (medially) and scutellar sutures absent (Fig. 12, 15); ovipositor bent upwards (Fig. 11); clypeus straight medially, above an indistinct hypoclypeal depression (Fig. 12) ..... *Mesostoinae* (p. 44)
- Mesoscutum not strongly protruding above pronotum, if exceptionally slightly protruding, then ovipositor straight or bent downwards; epistomal and clypeal sutures almost always complete; hypoclypeal depression absent, if present, then clypeus more or less concave and differently shaped (Fig. 27, 37) ..... 3
3. Hypoclypeal depression comparatively wide, deep and more or less round dorsally (Fig. 27, 28, 35, 37, 41), exceptionally the face takes part in the hypoclypeal depression (tribe *Pseudodicrogeniini*), resulting in a concave face and a flat clypeus (Fig. 121, 122); metasoma rather often sculptured, sometimes its second tergite with a semi-circular suture (Fig. 38) ..... 4
- Hypoclypeal depression absent, if present (Fig. 5, 52), then more or less shallow, narrower and straight dorsally or nearly so; face and clypeus more or less convex, not concave (Fig. 85, 86); metasoma (if intermediate) often smooth behind the first tergite (Fig. 63), its second tergite without semi-circular suture, at most with a more or less chevron-shaped impression (Fig. 63) ..... 8
4. Antenna situated at a protuberance, in front of the eyes (Fig. 97—99); venation of wings reduced (Fig. 105); maxillary palp with 4 segments; parasites of adult Coleoptera ..... tribe *Cosmophorini* of the *Euphorinae*
- Antenna more or less situated between the eyes (Fig. 25, 27, 34, 42), without distinctly developed protuberance; venation usually more complete (Fig. 19, 23, 31, 36, 43, 44); maxillary palp with 5 or 6 segments; parasites of larvae of various groups of insects ..... 5
5. First metasomal tergite strongly flattened basally and laterally (Fig. 22, 26); dorsope absent or nearly so, if present, then dorsal carinae are situated laterally, above the spiracles; prepectal carina absent; occipital carina absent dorsally; maxillary palpus with 5 segments, if with 6 segments (tribe *Histeromerini*, Fig. 25) then hind femur strongly compressed, disk-shaped (cf. Fig. 20) and fore tibia with a cluster of spines on two-third of its outer surface (Fig. 21);

- nervulus interstitial or nearly so (Fig. 23) or antefurcal (Fig. 19), very exceptionally postfurcal (Fig. 120) ..... Braconinae (p. 45)
- First tergite not or slightly flattened, usually with dorsope and/or dorsal carinae (Fig. 33, 38, 40, 46); dorsal carinae are removed from the spiracles; occipital carina usually (partly) present dorsally; prepectal carina variable; maxillary palp with 6 segments; hind femur not disk-shaped, at most weakly compressed; fore tibia with a row of spines (Fig. 32) or without spines (Fig. 39); nervulus usually postfurcal (Fig. 31, 36, 43, 44) or absent, exceptionally interstitial ..... 6
6. First metasomal tergite immovably joined to the second tergite, without dorsal carinae (Fig. 29, 30); three basal tergites about as long as half of metasoma . . . . . Telengainae (p. 45)
- First tergite flexibly joined to the second tergite, almost always with dorsal carinae, at least basally (Fig. 40); if exceptionally the first tergite is immovably joined to the second tergite, then the formed carapace is about as long as the metasoma ..... 7
7. Fore tibia with short, often rather thick spines (Fig. 32), if intermediate, then occipital and prepectal carinae complete; hind coxa usually with an antero-ventral tubercle; if nervulus is present, then sides of first brachial cell parallel (Fig. 36) ..... Doryctinae (p. 45)
- Fore tibia without spines (Fig. 39); occipital carina often partly, or completely absent; prepectal carina variable; hind coxa without tubercle; if intermediate then first brachial cell widened apicad (Fig. 43) and nervulus present ..... Rogadinae (p. 45)
8. Mandibles with inner side out, their tips not touching when closed (Fig. 48, 50); mandibles usually with 3—7 teeth or lobes (Fig. 49, 51), seldom with medial tooth large and both lateral teeth small ..... Alysinae (p. 46)
- Mandibles normal, their tips touching when closed (Fig. 5, 52, 85, 86, 90); mandibles with two teeth, exceptionally with three teeth ..... 9
9. Spiracles of first metasomal segment on its weakly sclerotized pleuron (Fig. 56, 59); prepectal and occipital carinae completely absent ..... Microgasterinae (p. 46)
- Spiracle of the first segment on its strongly sclerotized tergite (Fig. 61, 63, 77, 80, 82, 83); prepectal and occipital carinae variable ..... 10
10. Subdiscoidella present, often consisting of a more or less disconnected and yellowish or brownish stripe; nervellus often weakly pigmented posteriorly in respect to its anterior half (Fig. 65, 67, 73); if intermediate, then nervellus broken (Fig. 64) ..... 11
- Subdiscoidella absent (Fig. 74, 75, 79, 81, 84, 92); nervellus not broken, seldom its posterior half weakly pigmented in respect to the anterior half (Fig. 74, 92, 101) ..... 12
11. First discoidal cell sessile or subsessile (Fig. 65); cu 1 often absent; occipital carina completely absent; second tergite often with a chevron-shaped impression (Fig. 63); fore side of radial cell shorter than the pterostigma (Fig. 65) ...

- ..... Agathidinae (p. 47)
- First discoidal cell distinctly petiolate and cu 1 always present (Fig. 64, 67, 73); second tergite without chevron-shaped impression; fore side of radial cell equal in length to the length of pterostigma or somewhat longer (Fig. 64, 67, 73); occipital carina present, at least laterally ..... Meteorideinae (p. 47)
12. Postpectal and prepectal carinae completely present (Fig. 71); first metasomal tergite immovably joined to the second tergite, forming with the third tergite a rigid carapace (Fig. 72) ..... Cheloninae (p. 47)
- Postpectal carina absent (Fig. 87, 91), exceptionally a ventral remnant present; prepectal carina variable; first tergite usually movably joined to the second tergite (Fig. 78) ..... 13
13. First metasomal tergite flattened laterally and concave medially, almost invisible and immovably joined to the second tergite, forming with the third tergite a shield that covers slightly less than the basal half of the metasoma (Fig. 61); cuqu 1 from the pterostigma, usually far from r 1 (Fig. 62); transverse carina of propodeum strongly developed; occipital carina completely present ..... Acaeliinae (p. 47)
- First tergite distinctly convex (Fig. 53, 80, 83), if seldom somewhat flattened, then occipital carina absent; first tergite usually flexibly joined to the second tergite; if the first tergite is immovably connected, then the three basal tergites cover almost the complete length of the metasoma; cuqu 1 from the radius (Fig. 75, 79, 118); transverse carina of propodeum less developed ..... 14
14. Metasoma inserted above the hind coxae (Fig. 77, 78) ..... 15
- Metasoma inserted between the hind coxae, at least partly (Fig. 87, 91, 103, 106, 109) ..... 18
15. Metasoma inserted far above hind coxae (Fig. 78); occipital carina present dorsally ..... tribe Cenocoeliini of the Helconinae
- Metasoma inserted near hind coxae (Fig. 77); occipital carina absent dorsally ..... 16
16. Trochantellus with apical teeth externally (Fig. 77); submediellan cell large (Fig. 75, 81); middle lobe of mesoscutum more or less protruding (Fig. 76) ..... Macrocentrinae (p. 48)
- Trochantellus without apical teeth; submediellan cell small (cf. Fig. 23); middle lobe of mesoscutum not protruding ..... 17
17. Metapleural flange absent but with a rather wide and thin carina (cf. Fig. 91); radial cell comparatively wide (cf. Fig. 101); occipital carina present laterally ..... Orgilinae (p. 50)
- Metapleural flange present (cf. Fig. 78, 87); radial cell very narrow (cf. Fig. 65); occipital carina absent ..... Agathidinae (p. 47)
18. Maxillary palp short, with 2 or 3 segments (Fig. 3, 5); first brachial cell almost square (Fig. 4) or rqu present (Fig. 7); parasites of ants ..... 19
- Maxillary palp usually longer, with 4—6 segments; first brachial cell elongate and rqu absent; parasites of other groups ..... 20
19. First brachial cell almost square (Fig. 4); fore basitarsus very slender (Fig. 2);

- clypeus very narrow, longer than wide (Fig. 3); ovipositor straight; malar space concave posteriorly ..... Hybrizontinae (p. 48)
- First brachial cell elongate (Fig. 7); fore basitarsus stout (Fig. 6); clypeus wide, wider than long (Fig. 5); ovipositor strongly curved ventrad; malar space without concavity posteriorly ..... Neoneurinae (p. 49)
20. Nervellus absent and radial cell (so far present) moderately long (Fig. 93, 96); first brachial cell comparatively narrow (Fig. 93, 96); metasomal tergites weakly sclerotized (Fig. 95); first metasomal tergite usually slightly or not widened apicad; clypeus comparatively small (Fig. 94); pleural suture weakly developed; occipital carina present, at least laterally; parasites of aphids . . . . . Aphidiinae (p. 49)
- Nervellus present, if indistinctly developed or absent, then radial cell very short (Fig. 118), first brachial cell and clypeus wider; tergites distinctly sclerotized; first tergite and occipital carina variable; pleural suture usually wide and crenulate; parasites of other groups . . . . . 21
21. Basal vein strongly curved at its anterior end (Fig. 88); occipital carina completely absent . . . . . Ichneutinae (p. 49)
- Basal vein scarcely or not curved anteriorly (Fig. 92); occipital carina usually present laterally . . . . . 22
22. First tergite of metasoma flattened basally and laterally, without dorsal carinae (Fig. 82); occipital carina absent; anterior tentorial pits very large (Fig. 90); radial cell short and comparatively high (Fig. 92); basal vein more or less evenly bent; parasites of saw-flies . . . . . tribe Proteropini of the Ichneutinae (p. 49)
- First tergite scarcely or not flattened (Fig. 53, 83); occipital carina and/or dorsal carinae present; anterior tentorial pits much smaller (Fig. 52, 115); radial cell longer, if short, then narrow (Fig. 118); parasites of other groups . . . . . 23
23. Prepectal carina absent and metasoma short, oval (Fig. 53), its first tergite flexibly joined to the second tergite; hypoclypeal depression present or absent; notauli and precoxal suture more or less reduced; parasites of Diptera . . . . . Opiinae (p. 46)
- Prepectal carina almost always present; metasoma usually more slender (Fig. 111—113), sometimes tergite immovably joined to the second tergite; notauli and precoxal suture usually less reduced; almost always parasites of other groups . . . . . 24
24. First metasomal tergite petiolate (Fig. 111, 113), sometimes petiolus rather short (Fig. 112) or length more than 3.2 times its apical width (Fig. 114, 116); spiracle of first tergite usually situated medially or behind the middle of the tergite (Fig. 111, 114, 116) . . . . . 25
- First tergite sessile (Fig. 80, 83), shorter than 3.2 times its apical width; spiracle usually situated in front of the middle of first tergite (Fig. 80, 83) . . . . . 26
25. Radiellian cell widened distad (Fig. 107), sometimes with an interradiella; whole surface of 4th and 5th tergites of metasoma densely setose (Fig. 111);

- cuqu 2 present . . . . . tribe Zemiotini of the Zelinae (p. 50)
- Radiellan cell narrowed or scarcely widened distad, without interradiella (Fig. 117—119); if cuqu 2 present, then 4th and 5th tergites with one row of setae per tergite (Fig. 112, 113) . . . . . Euphorinae (p. 50)
26. Laterope deep (Fig. 109) and cuqu 2 absent, if intermediate, then ovipositor sheaths wide, shorter than three times its maximum width (Fig. 109) . . . . . tribe Centistini of the Euphorinae (p. 50)
- Laterope shallow (Fig. 87) or absent, if present then cuqu 2 present and/or ovipositor sheaths very slender, much longer than three times its maximal width . . . . . 27
27. Dorsal carinae of first tergite present, at least basally (Fig. 80, 83); if cuqu 2 absent and dorsal carinae of first tergite weakly developed, then dorsal surface of propodeum distinctly shorter than its posterior surface (Fig. 87) and radial cell comparatively wide (Fig. 84); mainly parasites of larvae of Coleoptera . . . . . Helconinae (p. 48)
- Dorsal carinae absent (Fig. 91, 103, 106), if present then cuqu 2 absent, dorsal surface of propodeum scarcely separated from its posterior surface and of more or less equal length (Fig. 91, 103, 106) and radial cell narrow (Fig. 101); parasites of Lepidoptera-larvae . . . . . 28
28. Anal lobe of hind wing distinctly developed and usually with a more or less developed aqu' (Fig. 100, 104), if aqu' absent, then metapleuron with a thin, more or less protruding carina (Fig. 103); distal abscissa of radius more or less curved (Fig. 100, 104) . . . . . Zelinae (p. 50)
- Anal lobe of hind wing comparatively narrow, without aqu' (Fig. 101, 102); if anal lobe is intermediate, then metapleuron without a thin carina, at most with a small flange (Fig. 106); distal abscissa of radius straight (Fig. 101, 102) . . . . . Orgilinae (p. 50)

#### SHORT DESCRIPTIONS OF THE SUBFAMILIES

##### ***Ypsistocerinae* (Fig. 8—10)**

Small subfamily, which contains the two genera *Ypsistocerus* Cushman and *Termitobracon* Brues. They live probably as parasites in the nests of termites in the Neotropical region. This group possesses many apomorphous characters, e.g., the unidentate mandibles (Fig. 10); the far retracted hypopygium (Fig. 8); the densely setose body (Fig. 8); the highly inserted antenna (Fig. 9) and the strongly reduced palpi and eyes (Fig. 9, 10).

##### ***Mesostoinae* (Fig. 11—18)**

Small subfamily, containing only the genus *Mesostoa* Van Achterberg from the Australian region, of which the biology is unknown. As pointed out by Van Achterberg (1975: 158) almost all characters are apomorphous, e.g., the absence of the occipital and prepectal carinae (Fig. 11); the absence of the precoxal and scutellar sutures (Fig. 11, 15); the flattened first metasomal tergite without carinae

(Fig. 14); the smooth propodeum; the concave frons (Fig. 18); the upcurved ovipositor and the compressed legs (Fig. 16).

### **Braconinae** (Fig. 19—27; 120—122)

Large subfamily, consisting of solitary or gregarious ectoparasites of larvae of holometabolous insects. The less evolved species often parasitize Coleoptera, the more evolved species also Lepidoptera, Hymenoptera-Symphyla and Diptera. According to Čapek (1970: 862) the host larva is paralysed at egg-deposition, the parasite-larva feeds on the paralysed host and forms its delicate cocoon at a sheltered place. The cephalic structures of the larvae are remarkably homogeneous. For the most parts none is reduced except for the mandibles, as in the main part of the Rogadinae as defined in the present paper. Therefore Čapek enlarged the concept of the Braconinae, in my opinion incorrectly because it is based on an aggregate of plesiomorphous characters. It only indicates that this group is less evolved than could be expected from the morphology of the adults. The adults have several apomorphous characters, e.g., the flattened first tergite (Fig. 22, 26); the reduction of the occipital and prepectal carinae and the maxillary palp consisting of 5 segments (except for the Histeromerini).

### **Telengainae** (Fig. 28—30)

Small subfamily containing only the Palaearctic genus *Telengaia* Tobias. The biology is unknown. The shape of the metasoma is peculiar (Fig. 29, 30), but I am not sure about its position; it may be only a member of the Rogadinae.

### **Doryctinae** (Fig. 31—36)

Rather large subfamily, consisting of ectoparasites of larvae of (wood-boring and bark-mining) Coleoptera. Less common also other hosts in plant tissues are attacked. The host-larva is paralysed before egg-deposition. The cephalic structures of the larvae are similar to those of the Braconinae. The morphology of the adults and their biology indicate their comparatively close relationship to the ancestral stem of the Braconidae. Some of the few apomorphous characters are the spines of the fore tibia (Fig. 32); the often large hypoclypeal depression (Fig. 35) and the usually distinctly developed dorsope (Fig. 33).

### **Rogadinae** (Fig. 37—44, 46)

As treated in the present paper a large group and rather heterogeneous because in this group the transition to endoparasitism has taken place. This is accompanied with some peculiarities as the tooth-less mandibles of the larvae (but already in the Braconinae occur larvae with only a few teeth on their mandibles) and the mummification of the host-caterpillar. In at least one genus closely related to *Rogas* Nees (viz., *Bucculatriplex* Viereck) the pupation takes place in the host-pupa in stead of in the mummified host-larva. Some species are solitary or

gregarious ectoparasites of larvae of Lepidoptera (*Hormius* Nees and its relatives; also *Oncophanes* Foerster, but *O. campsolechia* Watanabe (probably belonging to *Clinocentrus* Haliday) is reported to be a gregarious endoparasite of larvae of Lepidopterous leaf-rollers; their woolly cocoon is formed outside the host). Others are solitary ectoparasites of Hymenoptera-Symphyta (*Phanomeris* Foerster s.l.) or solitary endoparasites of mining larvae of holometabolous insects (*Colastes* Haliday), while *Rogas* Nees and its allied genera are mainly solitary or gregarious endoparasites of larvae of Lepidoptera, which pupate within the mummified larva or in the pupa. Some apomorphous characters are the often deep hypoclypeal depression; the reduction of the occipital carina in several genera; the endoparasitism of the main part of the subfamily and the often distinctly developed dorsope of the first metasomal tergite.

### Alysiinae (Fig. 45, 47—51)

One of the largest subfamilies of the Braconidae of which the larval cephalic structures, e.g., the simple and smooth mandibles, resemble those of the larvae of the Opiinae. Almost all species are solitary endoparasites of larvae of Diptera, but some are gregarious (*Aphaereta* Foerster). The egg is usually deposited in the larva, seldom in the egg (*Polemochartus* Schulz) or probably sometimes in the (pre-)pupa (*Aphaereta* Foerster). The delicate cocoon is made in the puparium of the host. The most striking apomorphous character of this group is the rotation of the mandibles of the adults in a way that the outer side becomes the inner side. Other apomorphous characters are the absence of the prepectal and the occipital carinae, together with the development of additional teeth on the mandible and of dorsope.

### Opiinae (Fig. 52, 53)

Rather large subfamily, consisting of endoparasites of larvae of Diptera; pupation in the puparium of the host. Closely related to the Alysiinae but the mandibles are normally attached (but more or less twisted) and the occipital carina is almost always present laterally. Some of its apomorphous characters are the smooth mandibles of the final instar larvae, the absence of the prepectal carina, the comparatively short and stout metasoma, the more or less reduced notauli, precoxal and pleural suturae and the tendency to develop a hypoclypeal depression.

### Microgasterinae (Fig. 54—60)

Large subfamily, consisting of endoparasites of larvae of Lepidoptera. Often gregarious; the eggs are deposited in the egg of the host or in the early instar larvae. In the Microgasterini and Cardiochilini the larvae pupate outside the host; the gregarious species often spin together in a common web. In the Miracini (which are endoparasites of leaf-mining Lepidoptera) the larvae pupate in the host-cocoon. The wing venation is often strongly reduced (Microgasterini, Mira-



cini), but the most important apomorphous characters are the position of the spiracle of the first metasomal segment and the absence of the prepectal and of the occipital carinae.

### **Agathidinae** (Fig. 64—66)

Rather large subfamily containing solitary or gregarious endoparasites of larvae of Lepidoptera. The egg is deposited in the early instar larva, the parasites pupate outside the host larva. The presence of a more or less distinct subdiscoidella (Fig. 65) and the sometimes comparatively high insertion of the metasoma are remarkable, but are probably old plesiomorphous characters; also the larvae are in several aspects (e.g., the shape of the mandibles) rather slightly derived. Some apomorphous characters are the small second cubital cell (or cuqu 2 absent), posterior half of nervellus more or less weakly pigmented; the absence of the occipital carina; the short radial cell (Fig. 65); and the second metasomal tergite often has a more or less chevron-shaped impression (Fig. 63).

### **Meteorideinae** (Fig. 63, 67, 68, 70, 73)

Small subfamily, solitary or gregarious endoparasites of larvae of Lepidoptera. According to Čapek (1970: 859) *Acampsis* Wesmael and *Sigalphus* Latreille may deposit their eggs in the egg of the host and pupate outside the host larva, while *Meteoridea* Ashmead pupates inside their host pupa. This group shows many plesiomorphous characters in both the larval and the adult morphology. Some of the few apomorphous characters are its endoparasitism, the comparatively wide ovipositor sheaths, the more or less developed dorsal carinae and deep laterope of the first metasomal tergite.

### **Cheloninae** (Fig. 69, 71, 72, 74)

Rather large subfamily, which consists of solitary endoparasites of larvae of Lepidoptera. The egg is deposited in the egg of the host. The delicate cocoon is attached to the remains of the host larva. This group possesses many apomorphous characters, e.g., the metasomal carapace, the short and high radial cell, the presence of the postpectal carina, the often densely setose eyes, the basally slender mandibles of the final instar larvae and the often indistinct hypostomal suture. The deposition of the egg in the host egg is clearly an adaptation to the habits of its hosts, which live at more or less hidden places.

### **Acaeliinae** (Fig. 61, 62)

Small subfamily, its members closely resemble the Miracini of the Microgasterinae (cf. Fig. 62 with Fig. 55). They share also their hosts, viz., both are endoparasites of larvae of leaf-mining Lepidoptera, also the pupation is in the cocoon of the host; this may account for their resemblance. The larvae are distinguishable from the larvae of the Microgasterinae by the presence of a mandibular base (cf.

Fig. 27, 28 in Čapek, 1970). The flattened shield formed by the three basal tergites of the metasoma is peculiar, they are fused almost invisibly (Fig. 61). Some other apomorphous characters are the strongly developed transverse carina of the propodeum, the position of the cuqu 1 and r 1 and the reduction of several other veins, e.g. the nervellus (Fig. 62).

### **Macrocentrinae (Fig. 75—77, 81, 86)**

Subfamily of moderate size, containing solitary or gregarious endoparasites of larvae of Lepidoptera. The parasite pupates outside the host. Polyembryony is known of the gregarious species, of which the specimens spin together in a common web. The most strikingly apomorphous character of this group is the toothed trochantellus (Fig. 77), others are the specialized depressed area at the second tergite laterally; the high attachment of the metasoma, the reduction of the occipital carina, the more or less protruding middle lobe of mesoscutum (Fig. 76) and the usually absent dorsal carinae of the first metasomal tergite (Fig. 77).

### **Hybrizontinae (Fig. 1—4)**

Small subfamily with one genus, *Hybrizon* Fallen, which contains endoparasites of larvae of several ant-genera. The naked pupae remain in the host nest. Possesses many apomorphous characters, e.g., the short palpi (Fig. 3), the concavity behind the malar space, the slender legs, the peculiar venation of the wings (Fig. 4), the slender clypeus and probably completely grown together 2nd and 3rd tergites (Fig. 1).

### **Helconinae (Fig. 78—80, 83—85, 87)**

Large subfamily of which almost all species are endoparasites of larvae of Coleoptera. The few exceptions may be *Blacus* Nees (some derived species have been bred from larvae of Diptera) and *Dyscoletes* Haliday (bred from larvae of Mecoptera). This subfamily is difficult to characterize by apomorphous characters, except for the endoparasitism. Formerly this name often served for a heterogeneous group, clearly used as a rest group of remaining genera. Actually the group of genera included in this paper can be characterized by several more or less "reticulate" occurring apomorphous characters. The most important apomorphous characters in the Cenocoeliini are the highly inserted metasoma (Fig. 78), the concave frons, as occurs also in the Helconini and less distinctly in the Brachistini. The Helconini (Fig. 83) have usually the dorsal carinae distinctly developed, often reaching behind the middle of the first tergite as in the Blacini (Fig. 80) and Brachistini. A dorsope is present in the Blacini (Fig. 80) and Cenocoeliini (Fig. 78), and less commonly in the Helconini (Fig. 83). The first discoidal cell is (sub-)sessile in the Helconini (p.p.), Brachistini (Fig. 84) and Blacini (but seldom shortly petiolate). The reduction of the veins aqu 1 + 2 and aqu' occurs in the Helconini, Brachistini and Blacini, as also the reduction of the sculpture on the metasoma and of the precoxal suture. The reduction of veins leads to the loss

of the cuqu 2 in the Brachistini (Fig. 84) and Blacini. In this subfamily the tribe Helconini is clearly less derived than other tribes; it possesses many plesiomorphous character-states. The final instar larvae have also many plesiomorphous characters (Fig. 9 in Čapek, 1970), which supports the hypothesis about the evolution of the Braconidae from exoparasites of sheltered living larvae of Coleoptera.

#### **Ichneutinae** (Fig. 82, 85, 88—90, 92)

Rather small subfamily, consisting of endoparasites of larvae of sawflies (Ichneutini, Proteropini) and of lepidopterous leafminers (Muesebeckiini). The egg is deposited in the egg of the host but the larva develops after pupation of the host. The cocoon is formed inside the cocoon of the host. Rather heterogeneous group, e.g., the final instar larvae of the Muesebeckiini have (at least in one genus) slender and smooth mandibles, stipital sclerite robust and hypostoma absent, while the Ichneutini have robust and toothed mandibles (as the Proteropini) and the cephalic sclerites present and robust (Fig. 33 in Čapek, 1970). The cephalic sclerites are also present in the Proteropini but are very slender (Fig. 32, l.c.). Also the imagines differ considerably, but with the information available it seems better to unite the three tribes in one subfamily. The most important apomorphous characters are the absence of the occipital carina, and also more or less of the prepectal carina in the Muesebeckiini and Proteropini; the short and comparatively high radial cell in the Ichneutini and Proteropini (Fig. 88, 92) (which resembles the Cheloninae), the short ovipositor with its more or less widened sheaths (Fig. 89), the more or less strongly curved basal vein and the absence of aqu' (Fig. 88, 92).

#### **Neoneurinae** (Fig. 5—7)

Small subfamily, consisting of endoparasites of adults of worker ants; the development is in the gaster of the host. The cocoon is attached to the remains of the host. The most important apomorphous characters are the short palpi (Fig. 5), the peculiar venation of the wings (Fig. 7), the concave coxae dorso-apically and the strongly bent ovipositor.

#### **Aphidiinae** (Fig. 93—96)

Rather large subfamily, containing solitary endoparasites of aphid nymphs and adults. *Praon* Haliday and *Dyscritulus* Hincks emerge from their host and spin their cocoon directly beneath the aphid, whereas all other genera pupate within the mummified host skin, mounted on the surface of the plant. The cephalic structures of the larvae are like those of other Braconidae, according to Čapek (1970, p. 848). The apomorphous characters of this subfamily are especially distinct in the larvae, because of the long and funnel-shaped spiracles without a division into atrium and closing apparatus, of the simple and smooth mandibles

and of the disk-shaped antennae. The apomorphous characters of the adults are the reduction of the wing venation (Fig. 93, 96), the specialized female genitalia and the weakly sclerotized metasoma (Fig. 95).

### **Zelinae** (Fig. 91, 100, 103, 104, 107, 111)

Small subfamily, which contains solitary endoparasites of larvae of Lepidoptera. The pupation is outside the host larva. The apomorphous character of the larvae in respect to the Orgilinae is the slender stipital sclerite; *Zemiotes* Foerster has also smooth mandibles and *Zelee* Curtis has the hypostomal spur absent. The adults have few apomorphous characters, e.g., the first metasomal tergite is slender and without dorsal carinae (Fig. 103), even petiolate in *Zemiotes* Foerster (Fig. 111).

### **Orgilinae** (Fig. 101, 102, 106)

Small subfamily containing species with often many apomorphous characters. They are endoparasites of larvae of Lepidoptera, which pupate outside the host larva; the emergence opening of the cocoon is irregular. The larvae are characterized by the absence of the hypostoma (Fig. 16, 17 in Capek, 1970). Apomorphous characters of the adult parasites are the absence of the aqu' (Fig. 101, 102); the more or less reduced metapleural flange (Fig. 106) and occipital carina dorsally; the more or less small radial cell of fore wing and anal lobe of the hind wing (Fig. 101, 102); cuqu 2 absent (Fig. 101) or if present, forming a small second cubital cell (Fig. 102).

### **Euphorinae** (Fig. 97, 99, 105, 108—110, 112—119)

Large and diverse subfamily, consisting of solitary or gregarious endoparasites of larvae of Lepidoptera and Coleoptera (*Meteorus* Haliday), of solitary or gregarious endoparasites of adult Coleoptera (and more seldom of their larvae), (e.g., *Perilitus* Nees s.l., *Ropalophorus* Haliday in Curtis, *Cryptoxilos* Viereck, *Streblocera* Westwood), of adult parasitic and aculeate Hymenoptera (*Syntretus* Foerster, the only exception to the rule that Braconidae are primary parasites), of adult Neuroptera (*Chrysopophthorus* Goidanich), of nymphal and adult Heteroptera (*Wesmaelia* Foerster, *Aridelus* Marshall, *Leiophron* Nees, *Holdawayella* Loan) and of nymphal and adult Psocoptera (*Leiophron* Nees). In *Meteorus* Haliday the cocoon of some species hangs from a long thread. The most important apomorphous character of the larvae are the smooth and short mandibles. The apomorphous characters of the adults are rather "reticulate" as in the Helconinae, e.g., the wing venation is reduced in the Cosmophorini (Fig. 105), the Euphorini (Fig. 118, 117, 119) and to a lesser degree in the Centistini, the parasitism of adult insects also occurs in these tribes; a dorsope occurs in the Centistini (p.p.), Euphorini (p.p.) (Fig. 110) and in the Meteorini (p.p.) (Fig. 112, 113); the notauli and the precoxal suture are reduced in the Centistini and in the Euphorini; the comparatively wide ovipositor sheaths, together with a more or less robust and bent ovipositor in the Centistini (Fig. 109) and Euphorini (p.p.; Fig. 108), and the

spiracles of the first metasomal tergite are situated in the middle of the tergite or behind the middle in the Euphorini (Fig. 110, 114, 116) and in the Meteorini (p.p.; Fig. 112, 113).

The possible relations between the subfamilies are depicted in Fig. 123. The following groups may be recognized:

Group A: The old "cyclostomes" of Wesmael, together with the later formed subfamilies Telengainae and Mesostoinae. They share the hypoclypeal depression, the apically more or less concave clypeus (Fig. 27, 28, 35, 41, 12, 37, 121) and the more or less flattened first metasomal tergite (Fig. 14, 22, 26, 30, 33, 38, 40).

Group B: Specialized endoparasites of larvae of Diptera with the pupation in the host-puparium. The larvae have smooth, sickle-shaped mandibles and the labial sclerite absent or at least broadly interrupted ventrally. The adults have the prepectal carina absent and a more or less oval metasoma (Fig. 53).

Group C: Specialized endoparasites of larvae of Lepidoptera; the egg is deposited in the eggs of the host or in the early instar larvae. The larvae of the Acaeliinae and of the Microgasterinae-Cardiochilini have the tips of the mandibles bifid; the larvae of the Microgasterinae and of the Cheloninae have mandibles without or only with a small, scarcely differentiated base. The adults often have the eyes densely setose, the radial vein is often shortened (Fig. 54, 55, 57, 58, 62, 74) and the first metasomal tergite is more or less flattened in the Microgasterinae and Acaeliinae (Fig. 56—61).

Group D: Specialized endoparasites of larvae of Lepidoptera; the larvae share the robust mandibles with a long, toothed blade (but the blade is intermediate in *Meteoridea* Ashmead). The imagines have the radial cell rather small (Fig. 65, 67, 73) and the laterope deep and usually large (Fig. 68, 70).

Group E: Specialized endoparasites of larvae of Lepidoptera; the larvae have the labial sclerite transverse and the epistomal arch and hypostoma are absent. The adults share the tendency to loose the dorsal carinae of the first metasomal tergite.

Group F: Generally very specialized endoparasites, especially of adult insects. The larvae have toothless, more or less wedge-shaped mandibles. The adults share the tendency to have the spiracle of the first metasomal tergite situated near the middle (Fig. 95, 109, 110, 112—114, 116); the wing venation is often very specialized (Fig. 7, 93, 96, 105, 117—119).

The position of the Hybrizontinae within the Braconidae is rather uncertain, the situation of the spiracle near the middle of the tergite (Fig. 1) it shares with group F, but this may be a convergent development.

The Ichneutinae, Macrocentrinae, and Helconinae form separate groups on their own. The larvae of the Ichneutinae show some similarity with the larvae in Group D, but the mandibles have a more or less developed triangular base. The adults also show some similarity, e.g., the reduction of the wing venation and the flattened first metasomal tergite in several groups.

The larvae of the Macrocentrinae have a transverse labial sclerite with two processes ventrally, and polyembryony occurs in the genus *Macrocentrus* Curtis. The adults differ from the Helconinae by the shape of the trochantellus (Fig. 77),

of the first and second metasomal tergites of the mesosoma (Fig. 76), and of the head (Fig. 86).

Finally the Helconinae; both in biology and morphology a slightly derived group. The larvae have wedge-shaped and toothed mandibles with a more or less distinctly differentiated base and the adults show the tendency to develop long dorsal carinae and distinct dorsope (Fig. 78, 80, 83).

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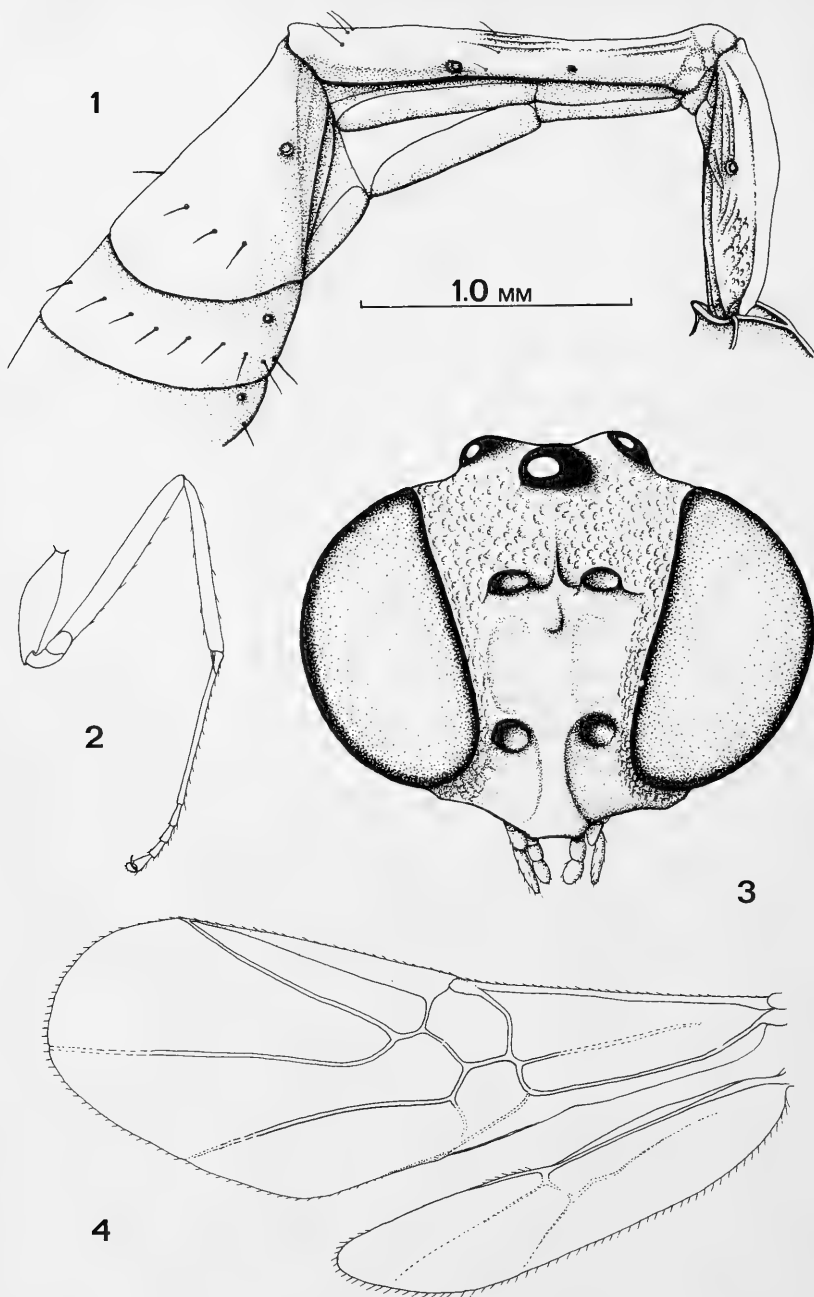


Fig. 1—4, *Hybrizon buccata* (de Brébisson), ♀, Netherlands, Meijendel. 1, basal half of metasoma, lateral aspect; 2, fore leg, lateral aspect; 3, head, frontal aspect; 4, wings. Fig. 1, 3: 2.1 times scaleline; Fig. 2, 4: scale-line



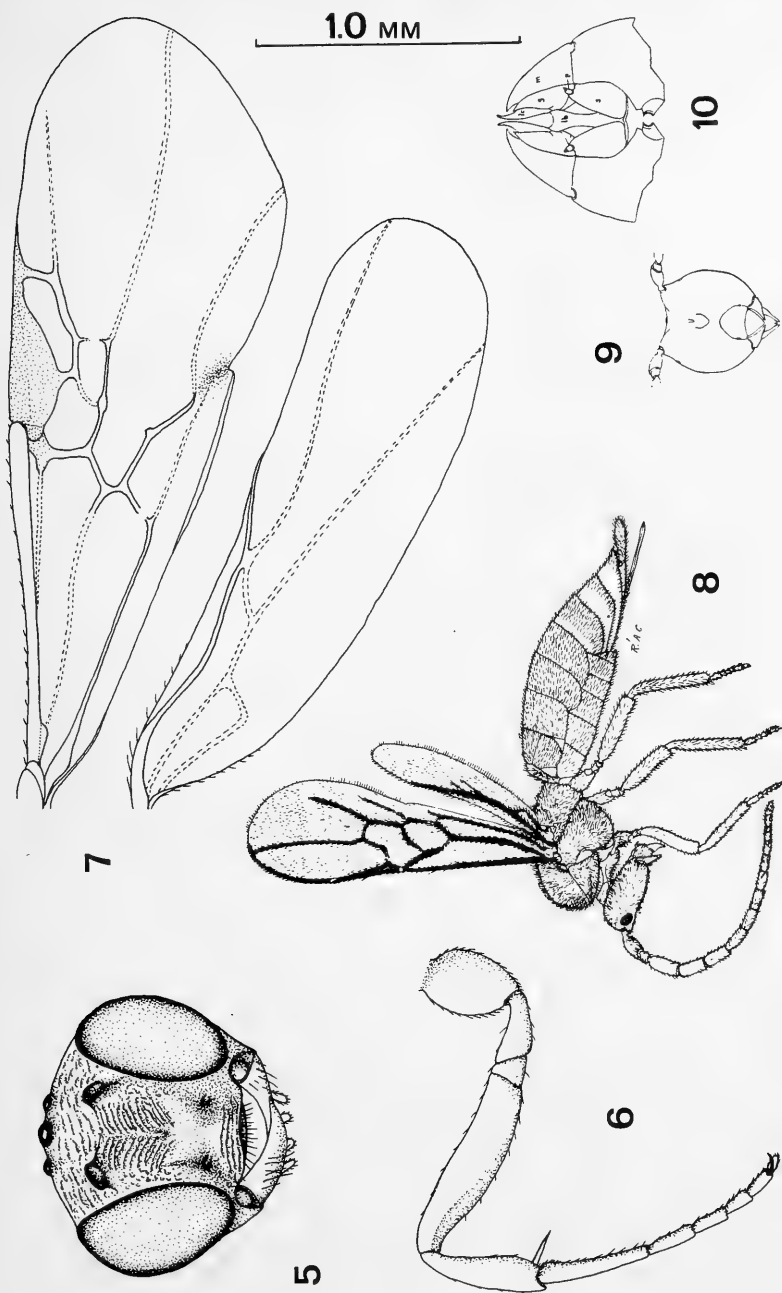


Fig. 5—7, *Neoneurus auctus* (Thomson), ♀, Lappland, Enontekiö. 5, head, frontal aspect; 6, fore leg, lateral aspect; 7, wings. Fig. 8, *Ypsistocerus manni* Cushman, ♀; habitus, lateral aspect. Fig. 9, 10, *Ypsistocerus vestigialis* Cushman. 9, head, frontal aspect; 10, mouth parts, ventral aspect. Fig. 5: scale-line; Fig. 6, 7: 1.2 times scale-line; Fig. 8: 0.5 times scale-line. Fig. 8-10 after Cushman, 1923

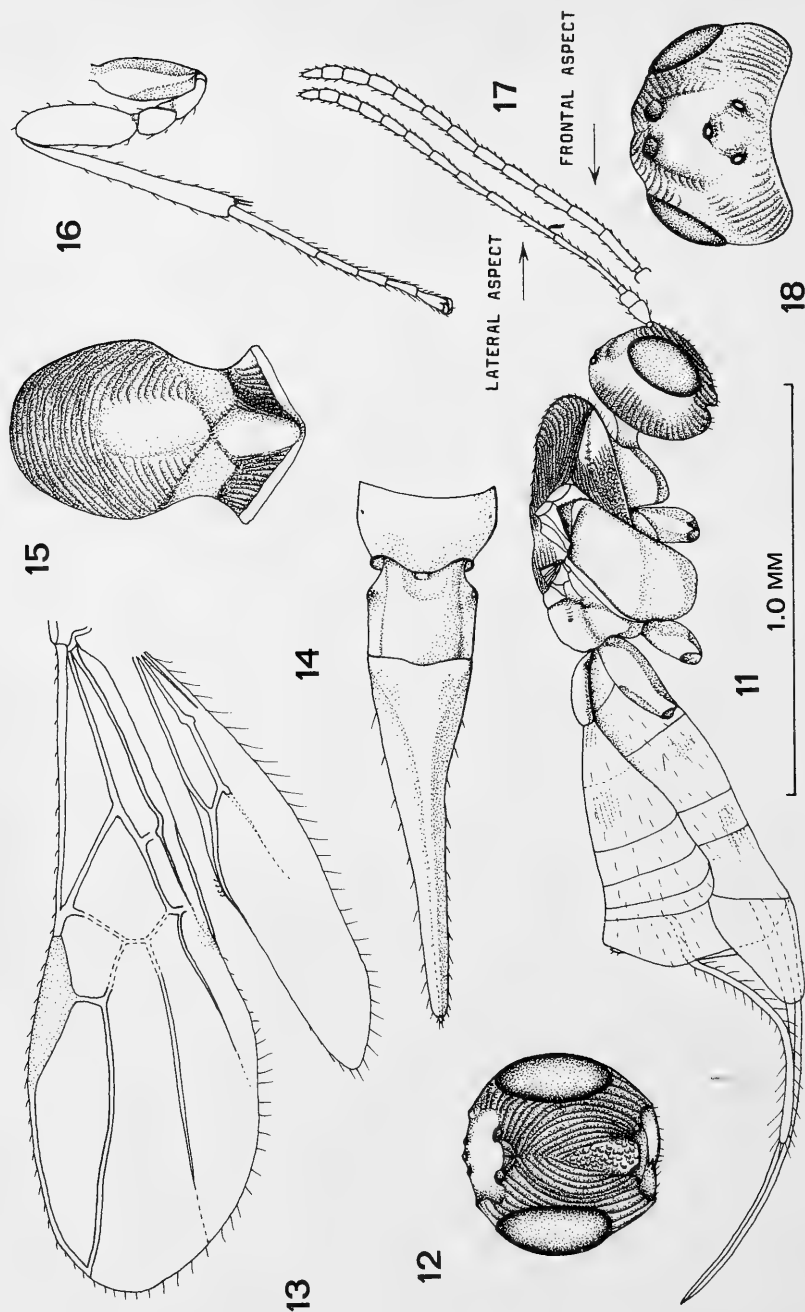


Fig. 11—18, *Mesostoa compressa* Van Achterberg, ♀, holotype. 11, habitus, lateral aspect; 12, head, frontal aspect; 13, wings; 14, abdomen, dorsal aspect; 15, mesonotum, dorsal aspect; 16, hind leg, lateral aspect; 17, antenna, frontal aspect; 18, head, dorsal aspect. Fig. 11, 13, 16, 17: scale-line; Fig. 12, 14, 15, 18: 1.5 times scale-line

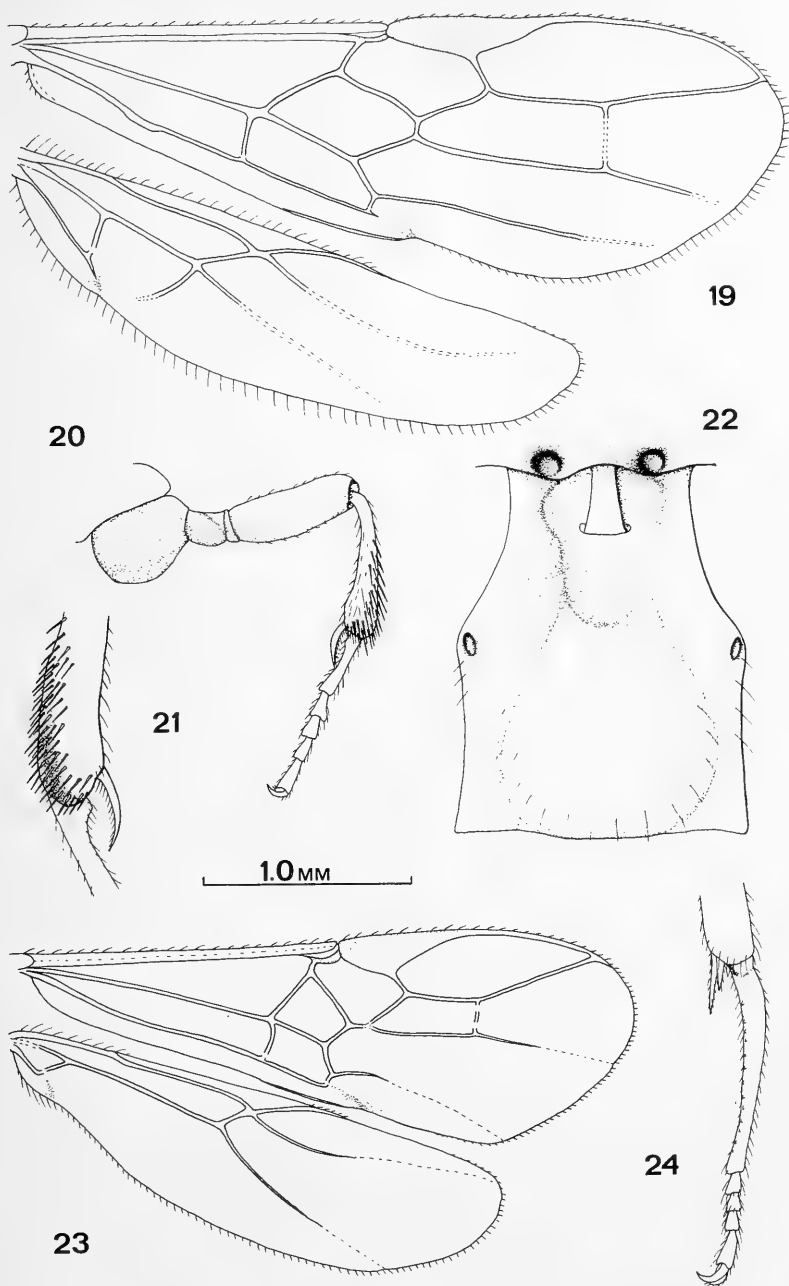


Fig. 19—21, 24, *Histeromerus mystacinus* Wesmael, ♀, Netherlands, Asperen. 19, wings; 20, fore leg, antero-lateral aspect; 21, detail of fore tibia, postero-lateral aspect; 24, hind tarsus, lateral aspect. Fig. 22, 23, *Bracon urinator* Fabricius, ♀, Switzerland, Saas-Fee. 22, first metasomal tergite, dorsal aspect; 23, wings. Fig. 19: scale-line; Fig. 20, 24: 1.2 times scale-line; Fig. 21, 22: 2.5 times scale-line; Fig. 23: 0.6 times scale-line

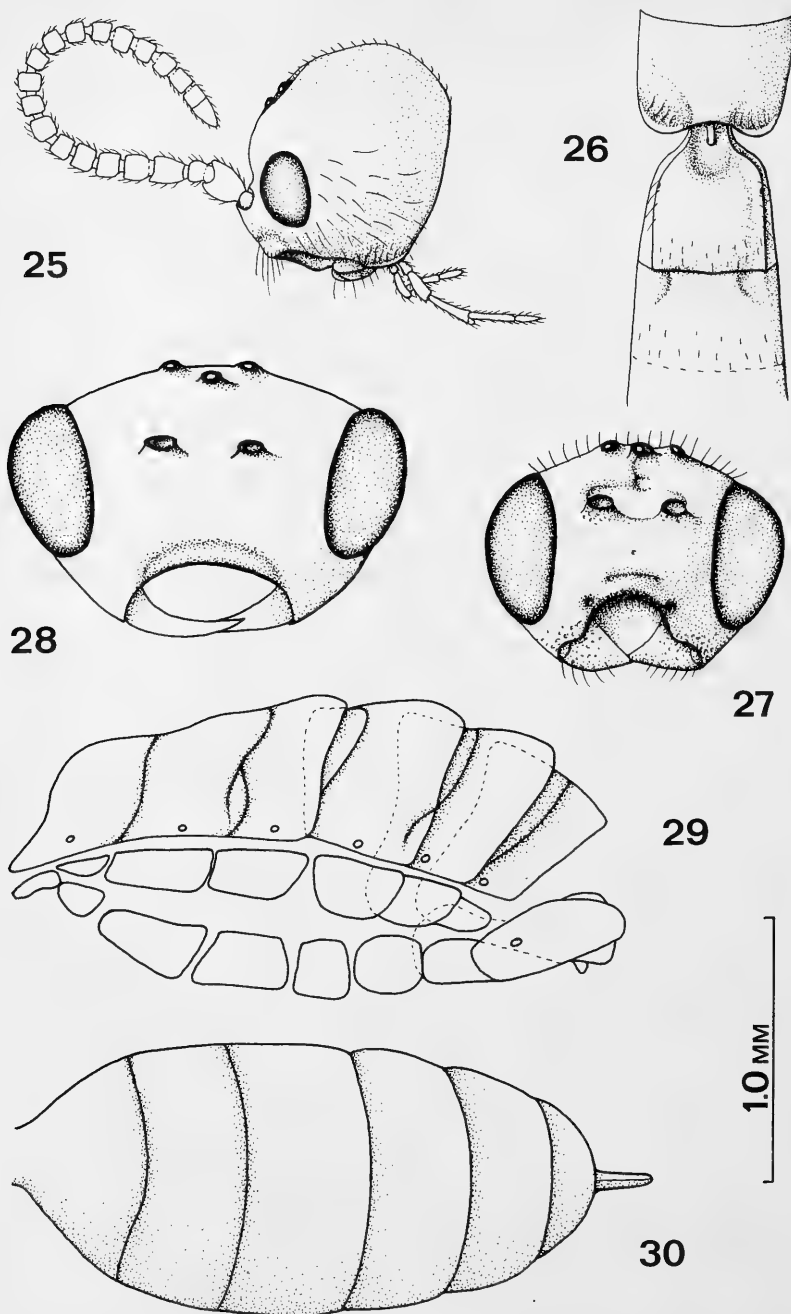


Fig. 25, 26, *Histeromerus mystacinus* Wesmael, ♀, Netherlands, Asperen. 25, head, lateral aspect; 26, propodeum, first and second metasomal tergites, dorsal aspect. Fig. 27, *Bracon urinator* Fabricius, ♀, Switzerland, Saas-Fee; head, frontal aspect. Fig. 28-30, *Telengaia ventralis* Tobias. 28, head, frontal aspect; 29, metasoma, lateral aspect; 30, metasoma, dorsal aspect. Fig. 25-27: scale-line; Fig. 28, 30: after Tobias, 1962; Fig. 29: after Tobias & Dudarenko, 1974

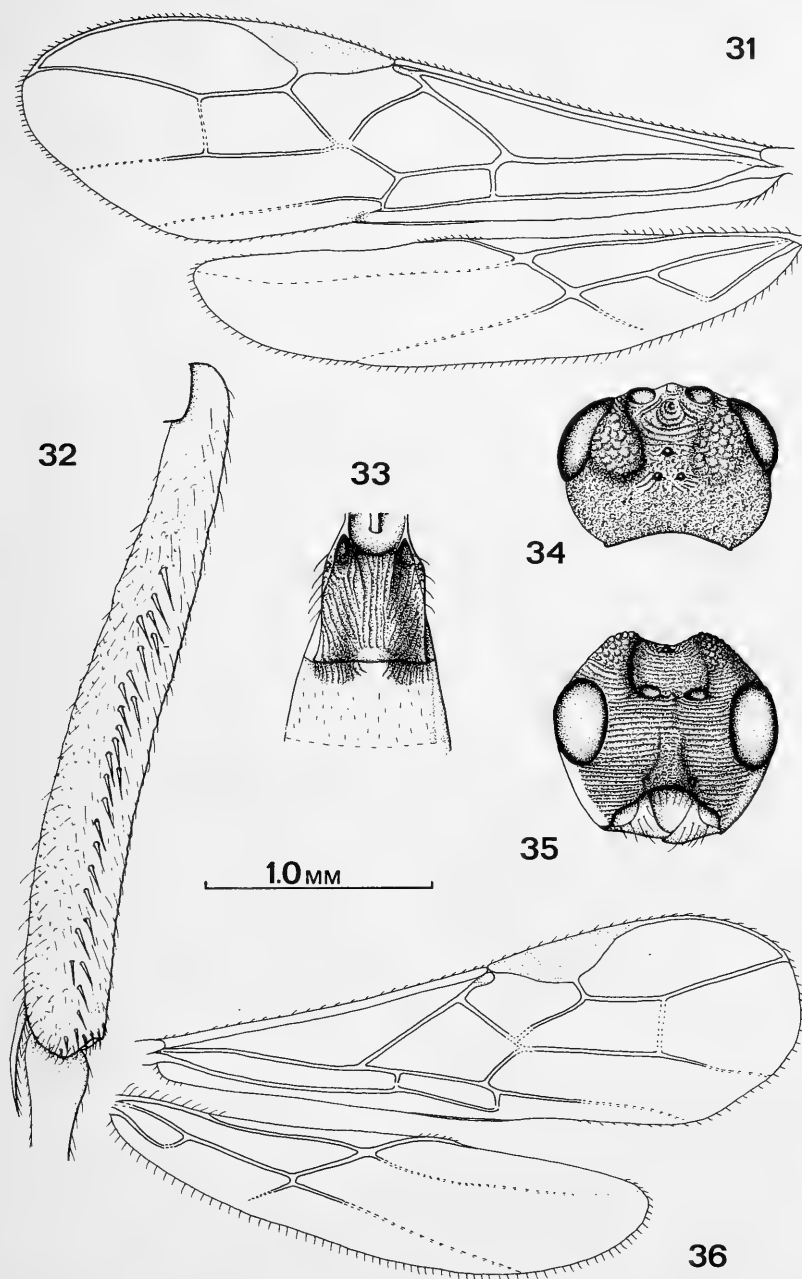


Fig. 31—33, *Doryctodes imperator* (Haliday), ♀, Netherlands, Cadier. 31, wings; 32, fore tibia, anterio-lateral aspect; 33, first and second metasomal tergites, dorsal aspect. Fig. 34—36, *Dendrosoter protuberans* (Nees), ♀, Netherlands, Best. 34, head, dorsal aspect; 35, head, frontal aspect; 36, wings. Fig. 31, 33: 0.6 times scale-line; Fig. 32: 2.5 times scale-line; Fig. 34—36: scale-line

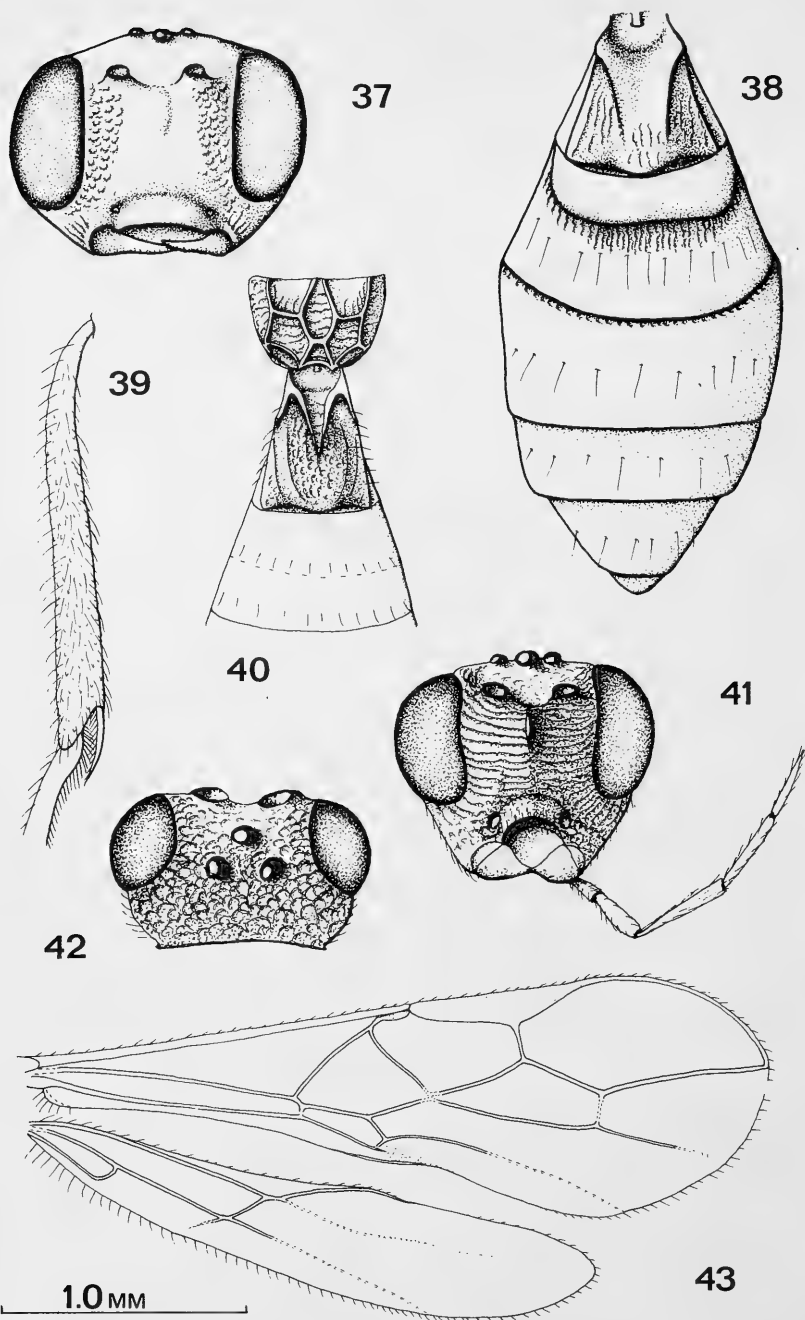


Fig. 37, 38, *Gnaptodon pumilio* (Nees), ♀, Netherlands, Waarder. 37, head, frontal aspect; 38, metasoma, dorsal aspect. Fig. 39, 40, 43, *Rhysalus clavator* Haliday, ♀, Netherlands, Wijster. 39, fore tibia, posterio-lateral aspect; 40, basal half of abdomen, dorsal aspect; 43, wings. Fig. 41, 42, *Rogas excavatus* (Telenga), ♂, Italy, Riva s. Garda. 41, head, frontal aspect; 42, head, dorsal aspect. Fig. 37-39: 2.5 times scale-line; Fig. 40-42: 1.2 times scale-line; Fig. 43: scale-line

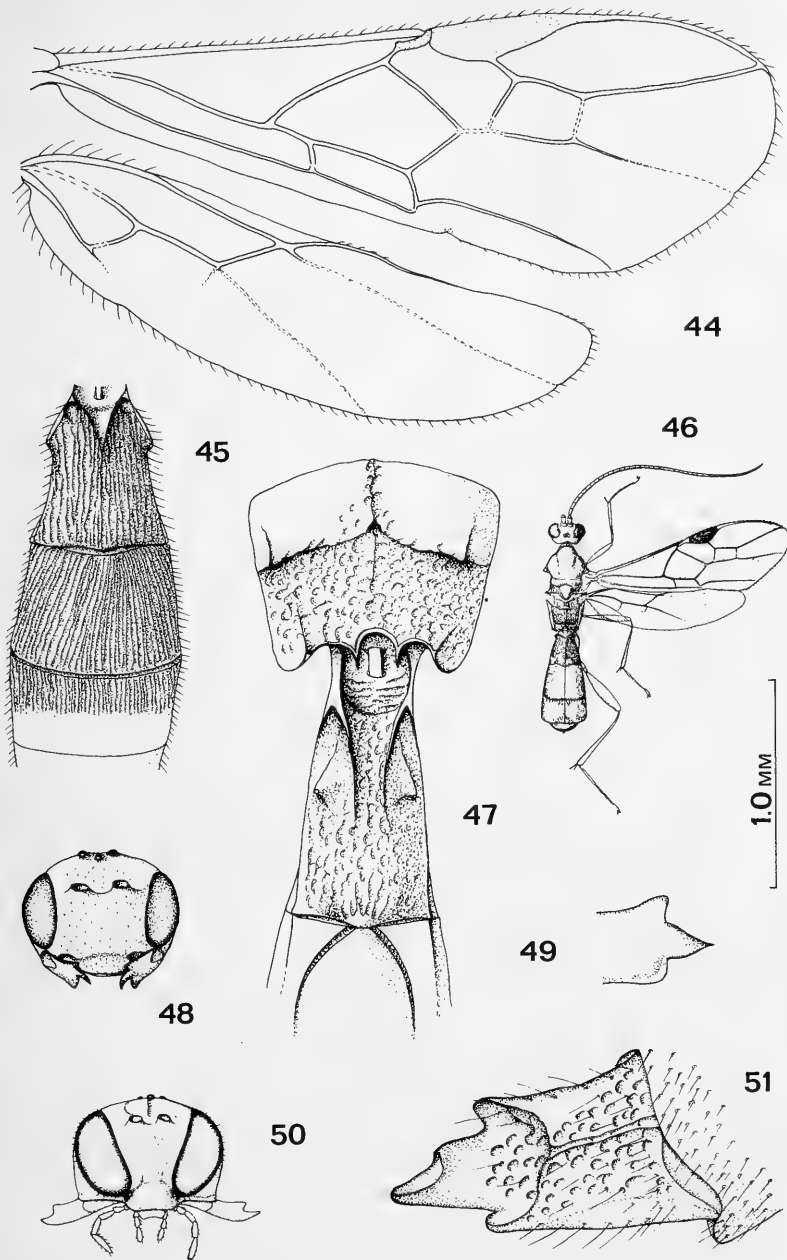


Fig. 44, *Rogas unipunctator* (Thunberg), ♀, Netherlands, Oostkapelle; wings. Fig. 45, 51, *Polemochartus liparae* (Giraud). 45, ♂, Netherlands, Haaren, three basal segments of metasoma, dorsal aspect; 51, ♀, Netherlands, Eindhoven, mandible, ventro-lateral aspect. Fig. 46, *Rogas drymoniae* Watanabe, 1937; habitus, dorsal aspect. Fig. 47-49, *Tanycarpa punctata* Van Achterberg, ♀, holotype. 47, propodeum, first and second metasomal tergites, dorsal aspect; 48, head, frontal aspect; 49, detail of mandible, lateral aspect. Fig. 50, *Chaenusa bergi* (Riegel), ♀, paratype; head, frontal aspect. Fig. 44, 45: 0.5 times scale-line; Fig. 46: 0.1 times scale-line; Fig. 47, 51: 2.5 times scale-line; Fig. 48: 1.2 times scale-line; Fig. 50: 1.8 times scale-line; Fig. 49: 3.2 times scale-line

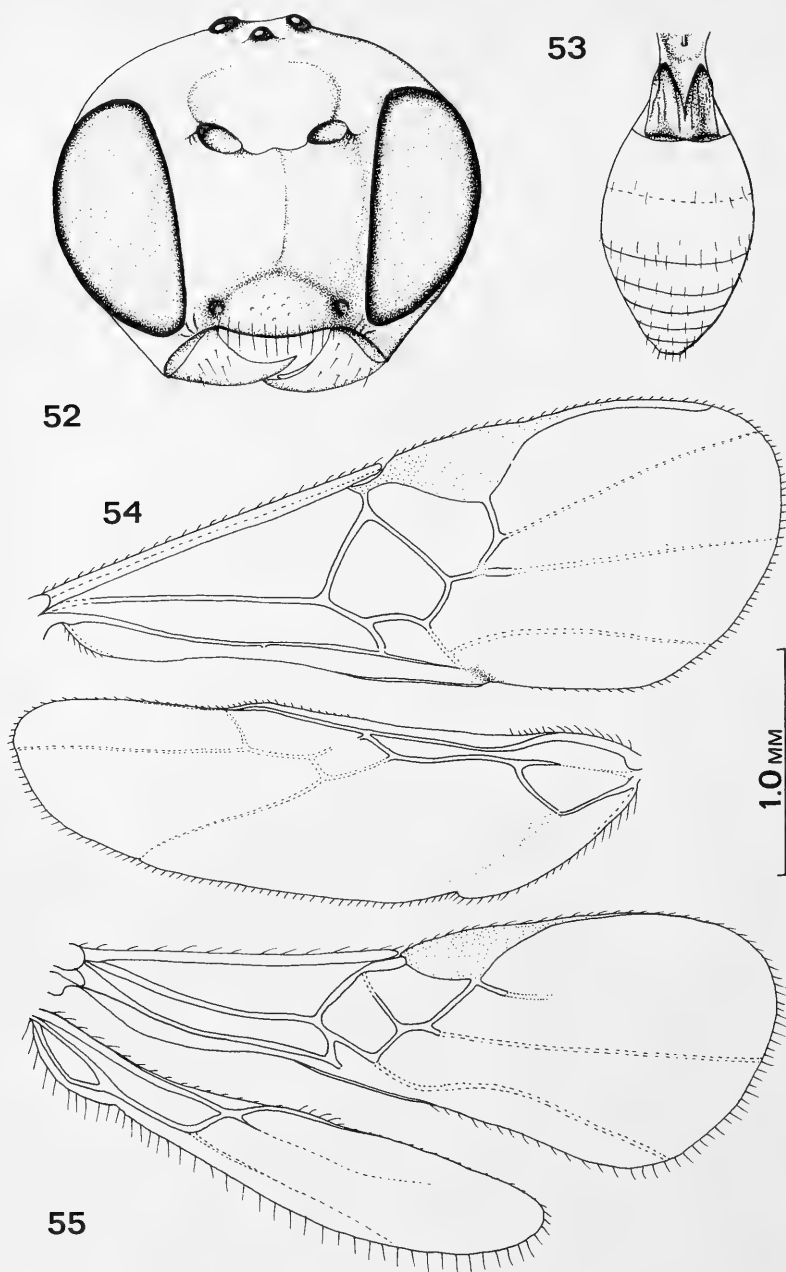


Fig. 52, 53, *Opius (Apodesmia) polyzonius* Wesmael, ♀, Netherlands, Asperen. 53, head, frontal aspect; 54, metasoma, dorsal aspect. Fig. 54, *Apanteles falcator* (Ratzeburg), ♀, Netherlands, Waarder; wings. Fig. 55, *Mirax cremastobombyciae* (Fullaway), ♀, holotype; wings. Fig. 52: 2.5 times scale-line; Fig. 53, 54: scale-line; Fig. 55: 1.7 times scale-line



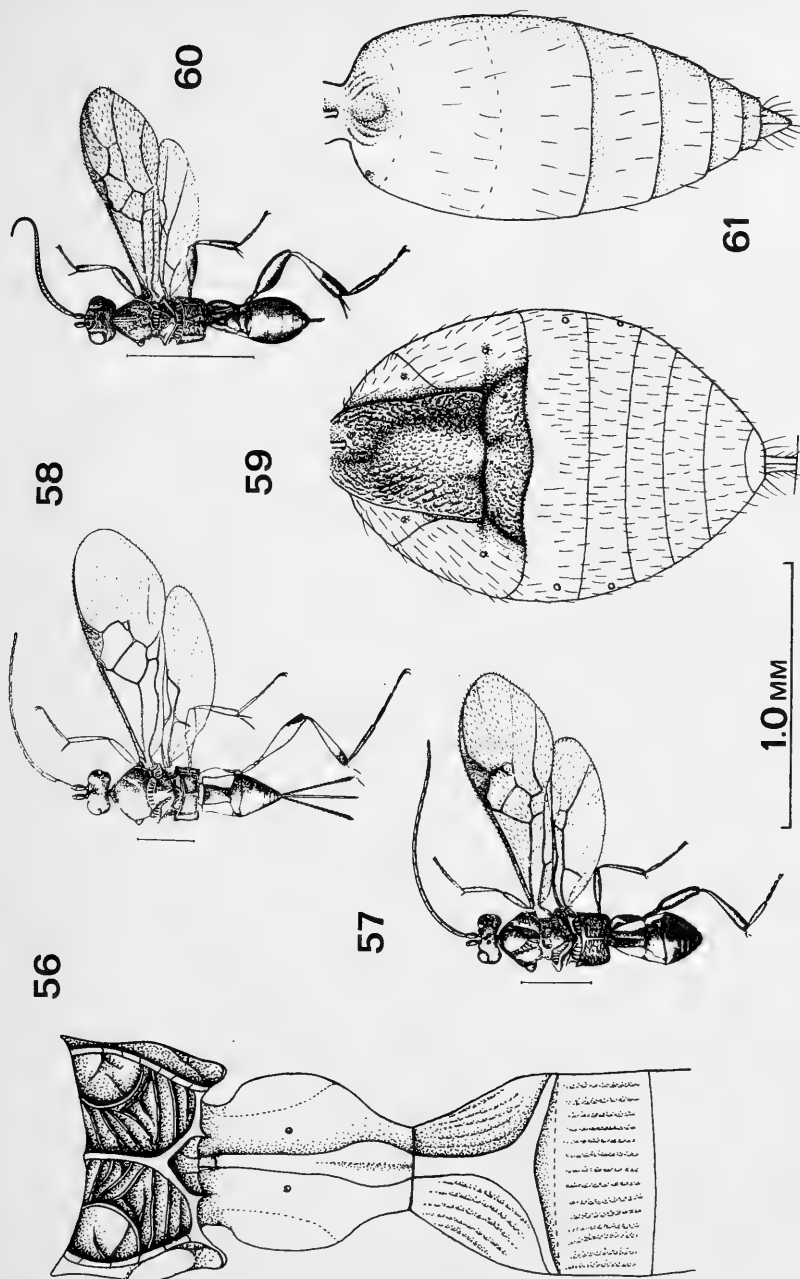


Fig. 56, *Mirax cremastobombyciae* (Fullaway), ♀, holotype; basal half of abdomen, dorsal aspect. Fig. 57, *Microplitis theretrae* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 58, *Microgaster takeuchii* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 59, *Apanteles falcator* (Ratzeburg), ♀, Netherlands, Waarder; metasoma, dorsal aspect. Fig. 60, *Cardiochiles japonicus* Watanabe, after Watanabe, 1937; habitus, dorsal aspect. Fig. 61, *Acaelius spec.*, ♀, Netherlands, Oostvoorne; metasoma, dorsal aspect. Fig. 56, 61: 2.5 times scale-line; Fig. 59: scale-line; Fig. 57, 58: 0.2 times scale-line; Fig. 60: 0.1 times scale-line

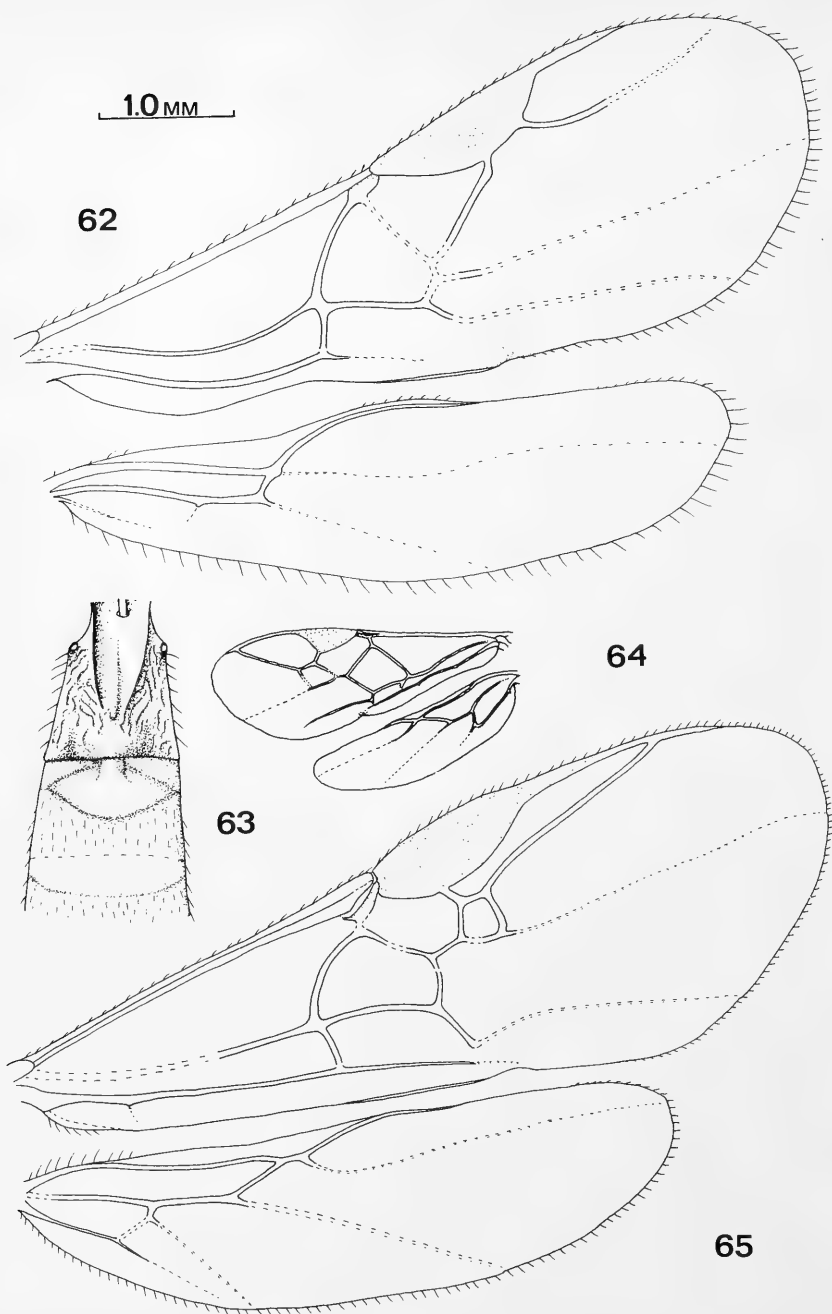


Fig. 62, *Acaelius spec.*, ♀, Netherlands, Oostvoorne; wings. Fig. 63, 65, *Earinus nitidulus* (Nees), ♀, Netherlands, Schaarsbergen. 63, first and second metasomal tergites, dorsal aspect; 65, wings. Fig. 64, *Meteoridea japonensis* Shenefelt & Muesebeck, after Shenefelt & Muesebeck, 1957; wings. Fig. 62: 4.0 times scale-line; Fig. 63, 65: scale-line

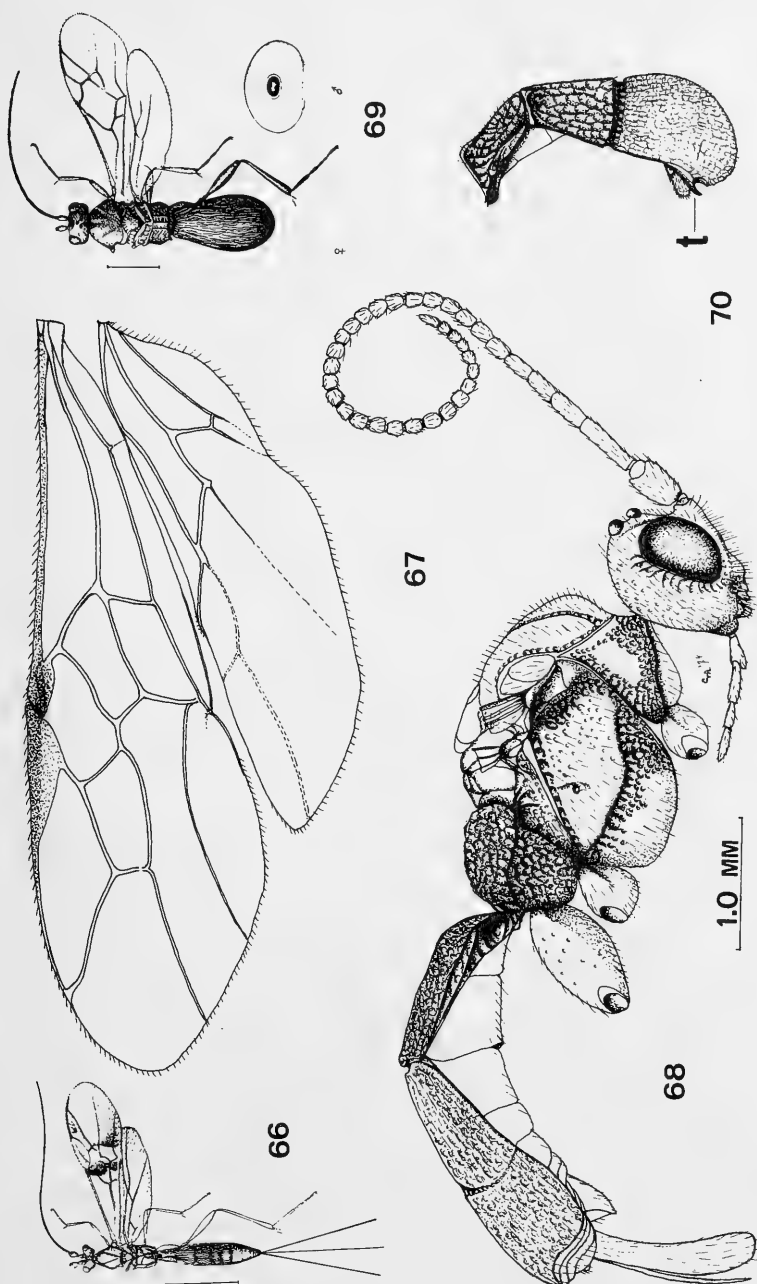


Fig. 66, *Braunsia matsumurai* Watanabe, ♀, after Watanabe, 1937; habitus, dorsal aspect. Fig. 67, 68, *Acampsis alternipes* (Nees), ♀, Netherlands, Den Haag. 67, wings; 68, habitus, lateral aspect. Fig. 69, *Chelonus (Microchelonus) tosenis* Watanabe, after Watanabe, 1937; ♀, habitus dorsal aspect; ♂, apex of metasoma, apical aspect. Fig. 70, *Sigalphus irrorator* (Fabricius), ♀, Netherlands, Naaldwijk; metasoma, lateral aspect. Fig. 66, 0.1 times scale-line. Fig. 67, 68, scale-line. Fig. 69, 0.4 times scale-line. Fig. 70, 0.6 times scale-line; t = tooth

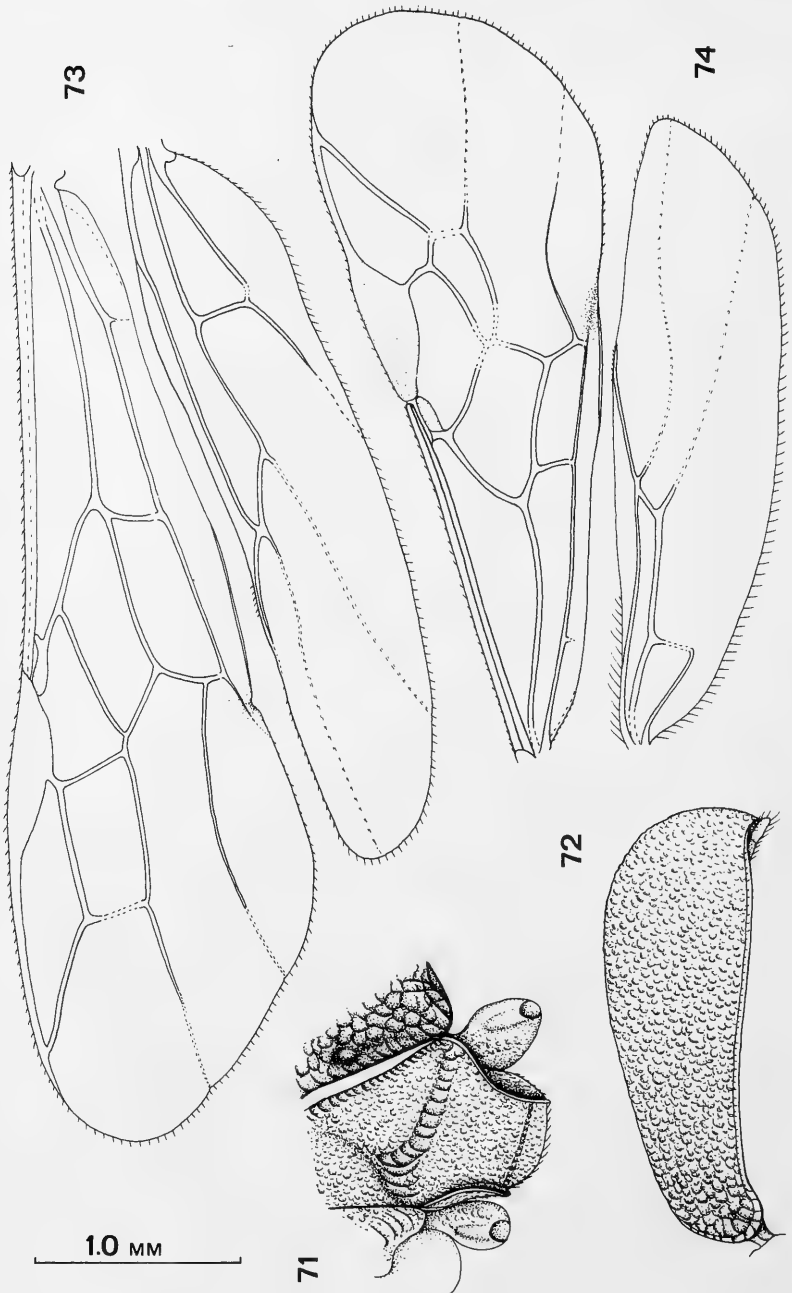


Fig. 71, 72, 74, *Ascogaster instabilis* Wesmael, ♀, Netherlands, Asperen. 71, mesosoma, ventro-lateral aspect; 72, metasoma, lateral aspect; 74, wings. Fig. 73, *Sigalphus irrorator* (Fabricius), ♀, Netherlands, Naaldwijk; wings. Fig. 71, 72, 74: scale-line; Fig. 73: 0.5 times scale-line

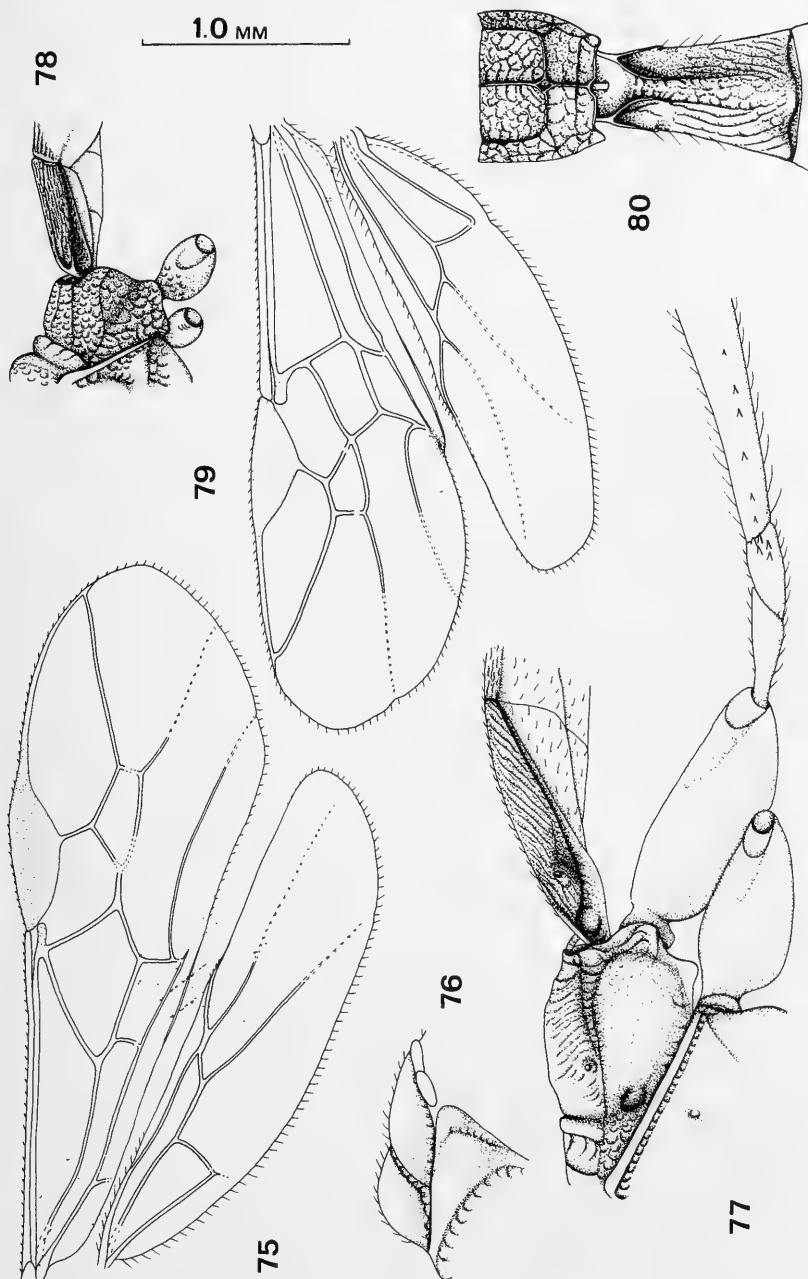


Fig. 75—77, *Macrocentrus thoracicus* (Nees), ♀, Netherlands, Meijndel. 75, wings; 76, mesoscutum, lateral aspect; 77, propodeum and first metasomal segment, lateral aspect. Fig. 78, 79, *Cenocoelius analis* (Nees), ♀, Netherlands, Wijster. 78, propodeum and first metasomal segment, lateral aspect; 79, wings. Fig. 80, *Blacus (Ganychorus) striatus* Van Achterberg, ♀, holotype; propodeum and first metasomal tergite, dorsal aspect. Fig. 75: 0.5 times scale-line; Fig. 76-79: scale-line; Fig. 80: 2.5 times scale-line

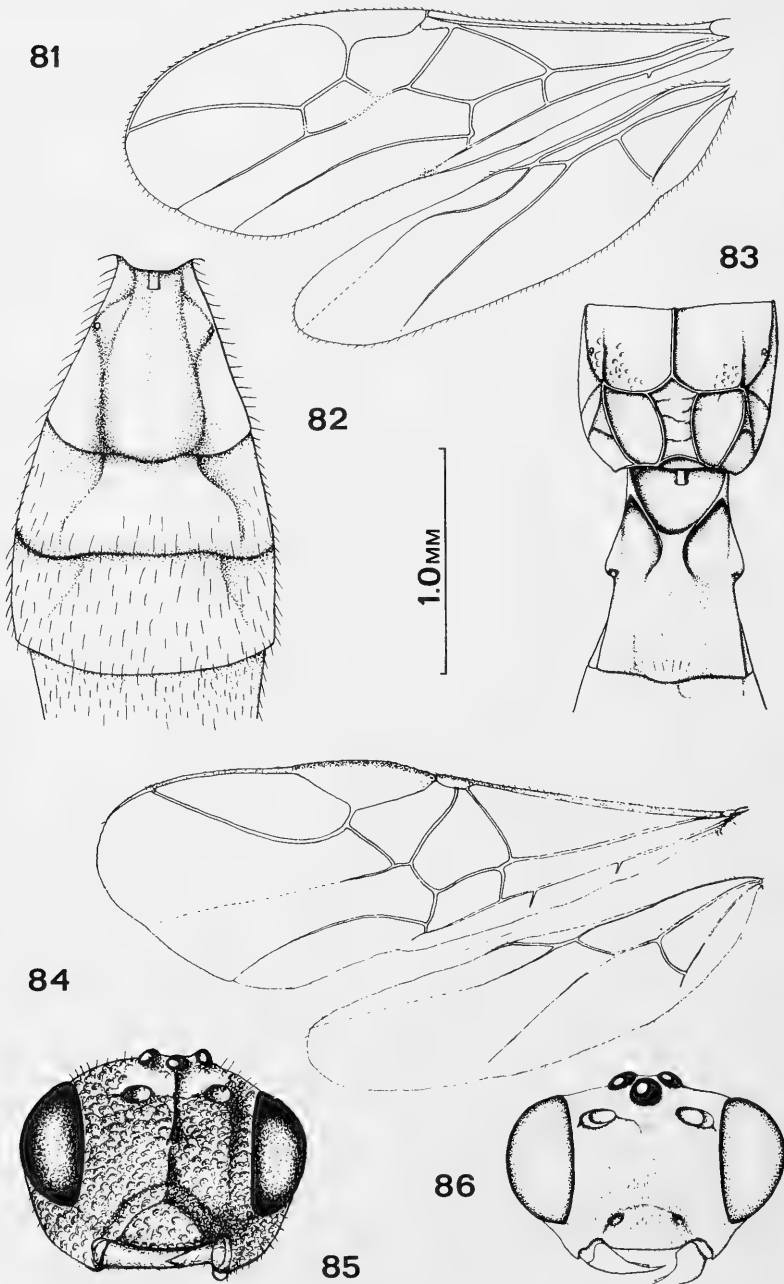


Fig. 81, 86, *Austrozele breviceaudis* (Szépligeti), ♀, lectotype. 81, wings; 86, head, frontal aspect. Fig. 82, *Proterops nigripennis* Wesmael, ♀, Netherlands, Kralo; basal half of metasoma, dorsal aspect. Fig. 83, *Elachistocentrum similis* (Szépligeti), ♀, lectotype; propodeum and first metasomal tergite, dorsal aspect. Fig. 84, *Eubazus* (*Brachistes*) *lapponicus* (Thomson), ♀, lectotype; wings. Fig. 85, *Ichneutes* spec., ♀, Netherlands, Waarder; head, frontal aspect. Fig. 81: 0.4 times scale-line; Fig. 82: scale-line; Fig. 83: 1.8 times scale-line; Fig. 84: 0.7 times scale-line; Fig. 85: 1.2 times scale-line; Fig. 86: 0.8 times scale-line

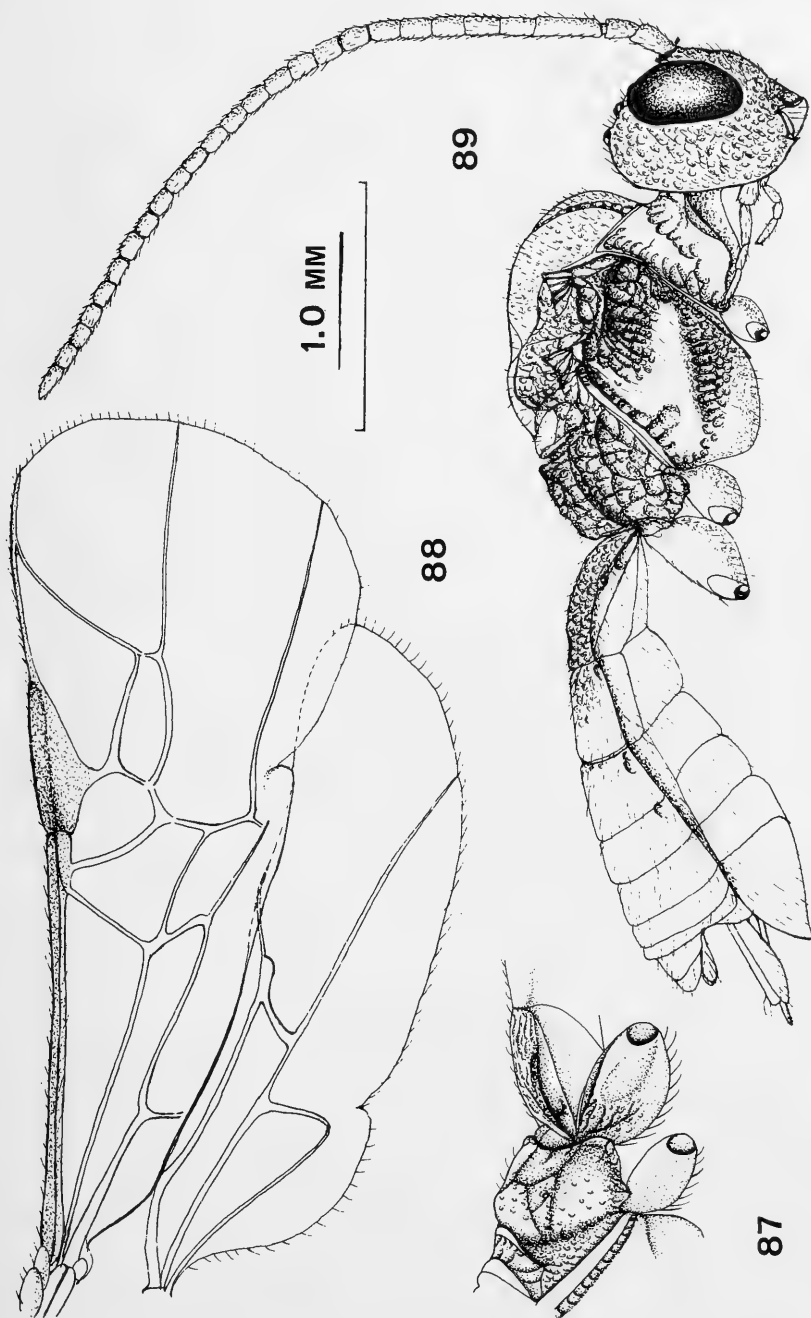


Fig. 87, *Eubazus (Foersteria) tibialis* (Haliday), ♂, Netherlands, Wijster; propodeum and first metasomal segment, lateral aspect. Fig. 88, 89, *Ichneutes* spec., ♀, Netherlands, Waarder. 88, wings; 89, habitus, lateral aspect. Fig. 87-89: scale-line

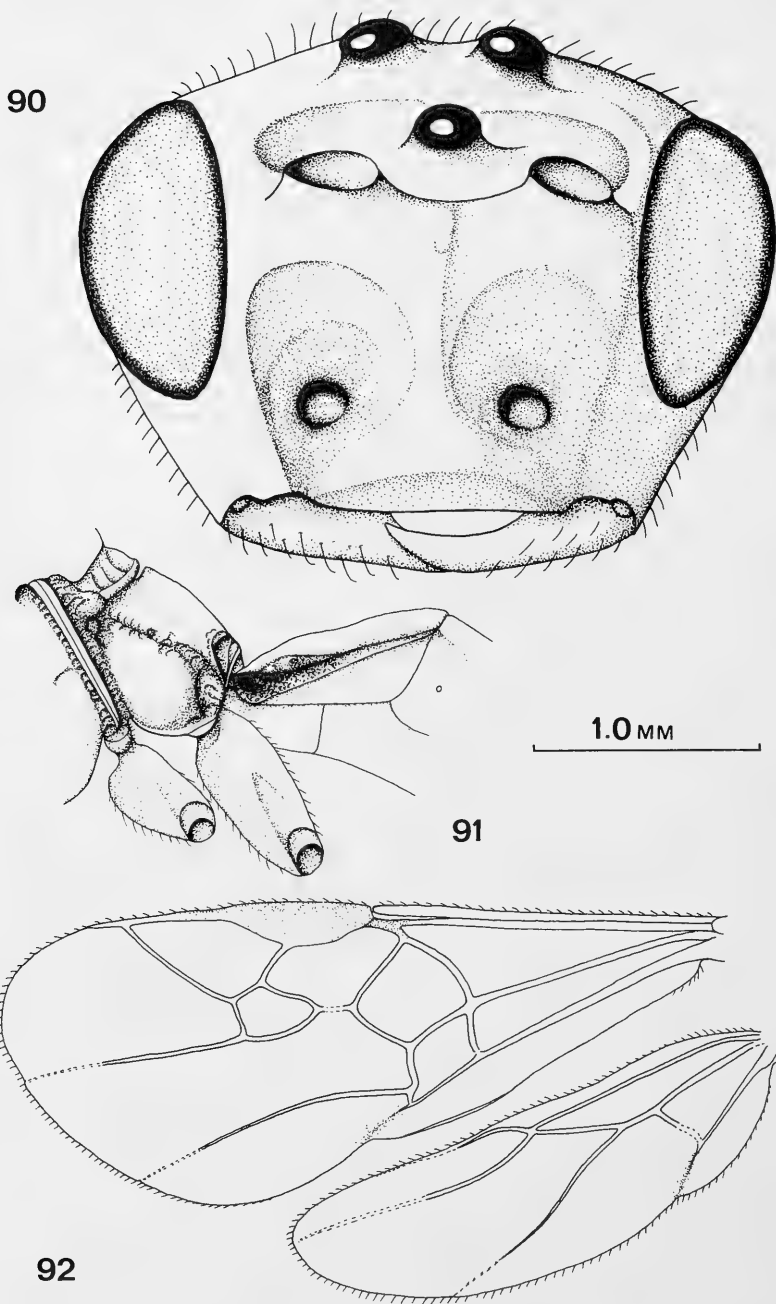


Fig. 90, 92, *Proterops nigripennis* Wesmael, ♂, Netherlands, Kralo. 90, head, frontal aspect; 92, wings. Fig. 91, *Charmon extensor* (Linnaeus), ♀, Netherlands, Naardermeer; propodeum and first metasomal segment, lateral aspect. Fig. 90: 2.5 times scale-line; Fig. 91: scale-line; Fig. 92: 0.6 times scale-line



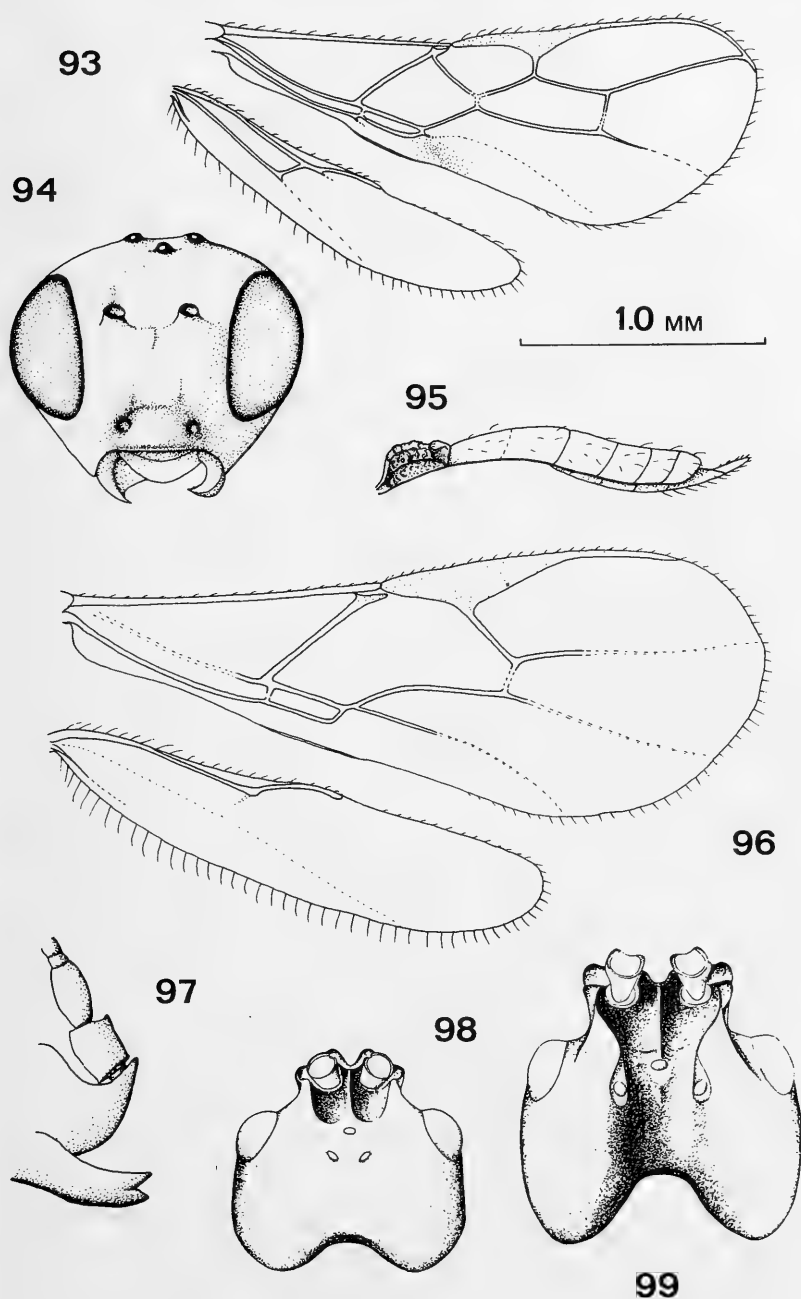


Fig. 93—95, *Ephedrus plagiator* (Nees), ♀, Netherlands, Maastricht. 93, wings; 94, head, frontal aspect; 95, metasoma, lateral aspect. Fig. 96, *Aphidius ervi* Haliday, ♀, Netherlands, Asperen; wings. Fig. 97, *Cosmophorus cembrae* Ruschka, after Hedqvist, 1955; anterior part of head, lateral aspect. Fig. 98, *Cosmophorus klugi* Ratzeburg, after Watanabe, 1968; head, dorsal aspect. Fig. 99, *Cosmophorus regius* Niezabitowski, id. Fig. 93, 95, 96: scale-line; Fig. 94: 2.5 times scale-line

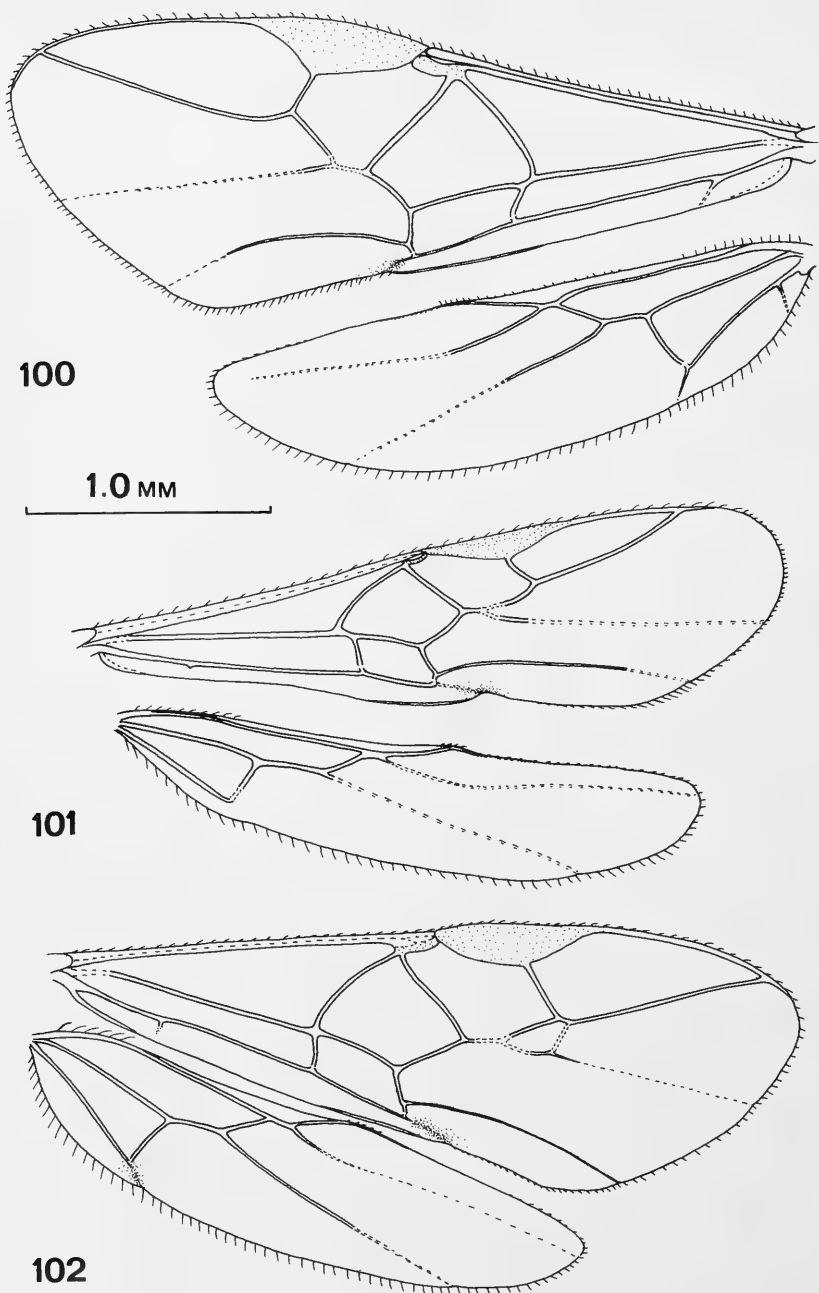


Fig. 100, *Charmon extensor* (Linnaeus), ♀, Netherlands, Naardermeer; wings. Fig. 101, *Orgilus laevigator* (Nees), ♀, Netherlands, Waarder; wings. Fig. 102, *Microtypus wesmaeli* Ratzeburg, ♀, Netherlands, Craillo; wings. Fig. 100, 102: 0.6 times scale-line; Fig. 101: scale-line

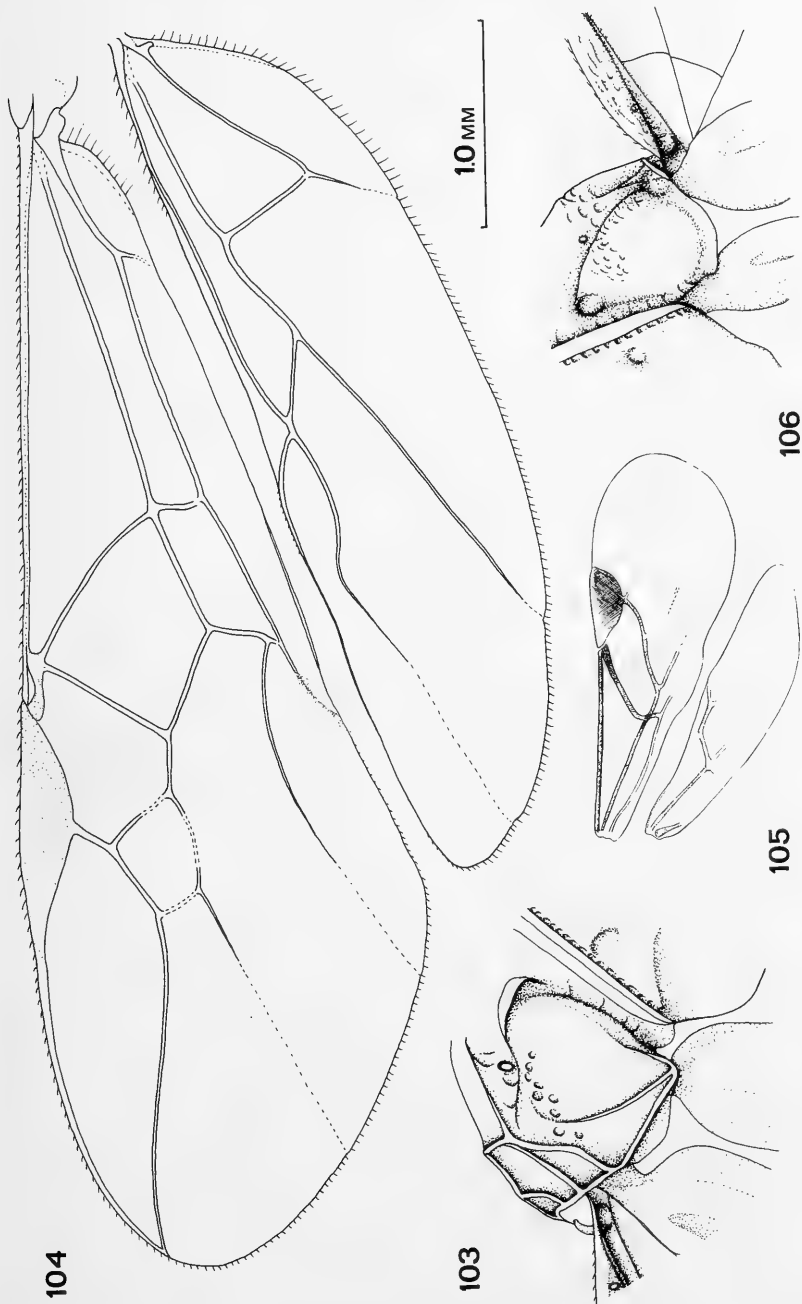


Fig. 103, 104, *Zele infumator* Lyle, ♀, Netherlands, Crailo. 103, Propodeum, lateral aspect; 104, wings.  
 Fig. 105, *Cosmophorus regius* Niezabitowski, after Watanabe, 1968; wings. Fig. 106, *Microtypus wesmaeli*  
 Ratzeburg, ♀, Netherlands, Crailo; propodeum, lateral aspect. Fig. 103, 104: 0.6 times scale-line;  
 Fig. 106: scale-line

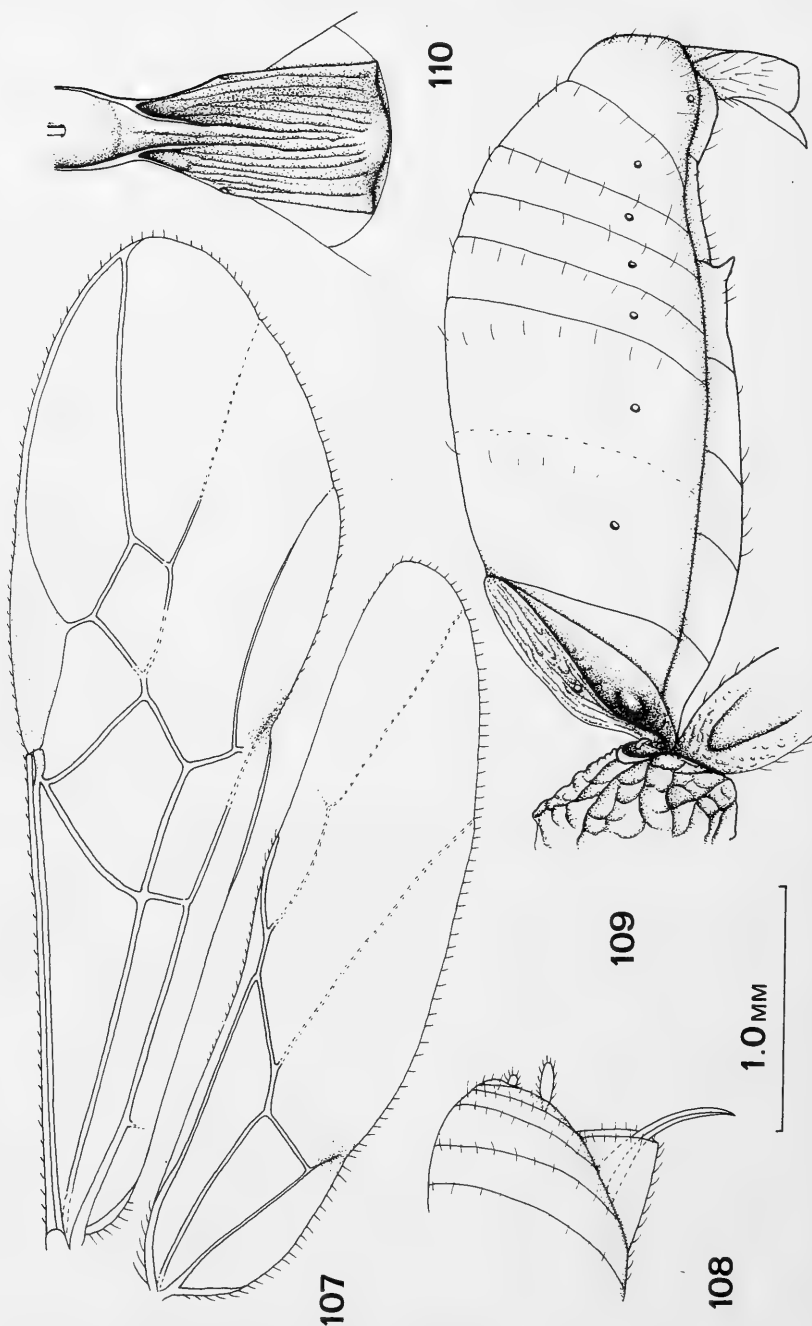


Fig. 107, *Zemiotes deceptor* (Wesmael), ♀, Netherlands, Wageningen; wings. Fig. 108, *Leio-phron* (*Leio-phron*) *apicalis* Haliday, ♀, Netherlands, Wijster; apex of metasoma, lateral aspect. Fig. 109, *Ancylo-centrus ater* (Nees), ♀, Netherlands, Waarder; metasoma, lateral aspect. Fig. 110, *Streblocera macro-scapa* (Ruthe), ♀, Netherlands, Waarder; first metasomal tergite, dorsal aspect. Fig. 107: 0.6 times scale-line; Fig. 108-110: 2.5 times scale-line

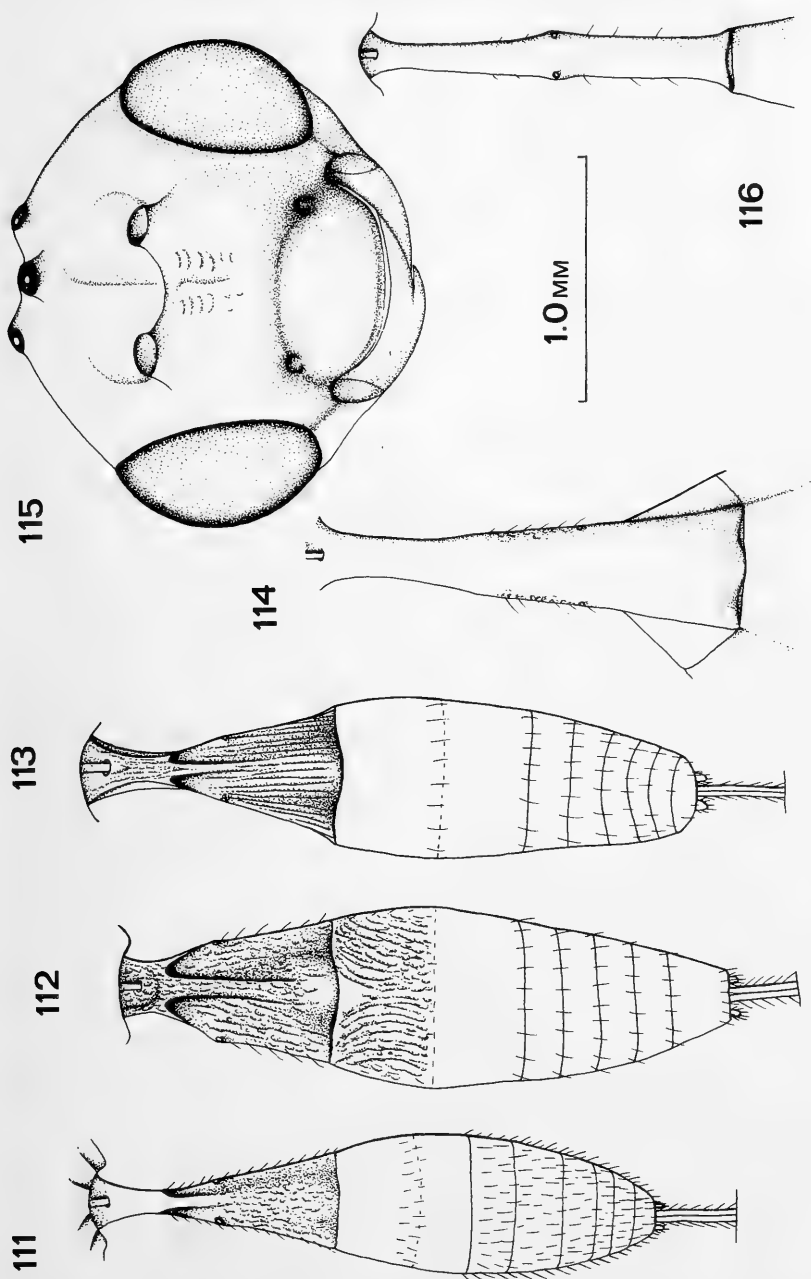


Fig. 111, *Zemites deceptor* (Wesmael), ♀, Netherlands, Wageningen; metasoma, dorsal aspect. Fig. 112, *Meteorus* cf. *sulcatus* Szépligeti, ♀, Netherlands, Wijster; metasoma, dorsal aspect. Fig. 113, *Meteorus ictericus* (Nees), ♀, Netherlands, Waarder; metasoma, dorsal aspect. Fig. 114, *Syntretus* cf. *conterminus* (Nees), ♀, Netherlands, Waarder; first metasomal tergite, dorsal aspect. Fig. 115, *Perilitus* (*Microctonus*) cf. *deceptor* Wesmael, ♀, Netherlands, Putten (G.); head, frontal aspect. Fig. 116 *Chrysopophthorus* spec., ♀, Costa Rica, Turrialba; first metasomal tergite, dorsal aspect. Fig. 111: 0.6 times scale-line; Fig. 112, 113, 116: scale-line; Fig. 114, 115: 2.5 times scale-line

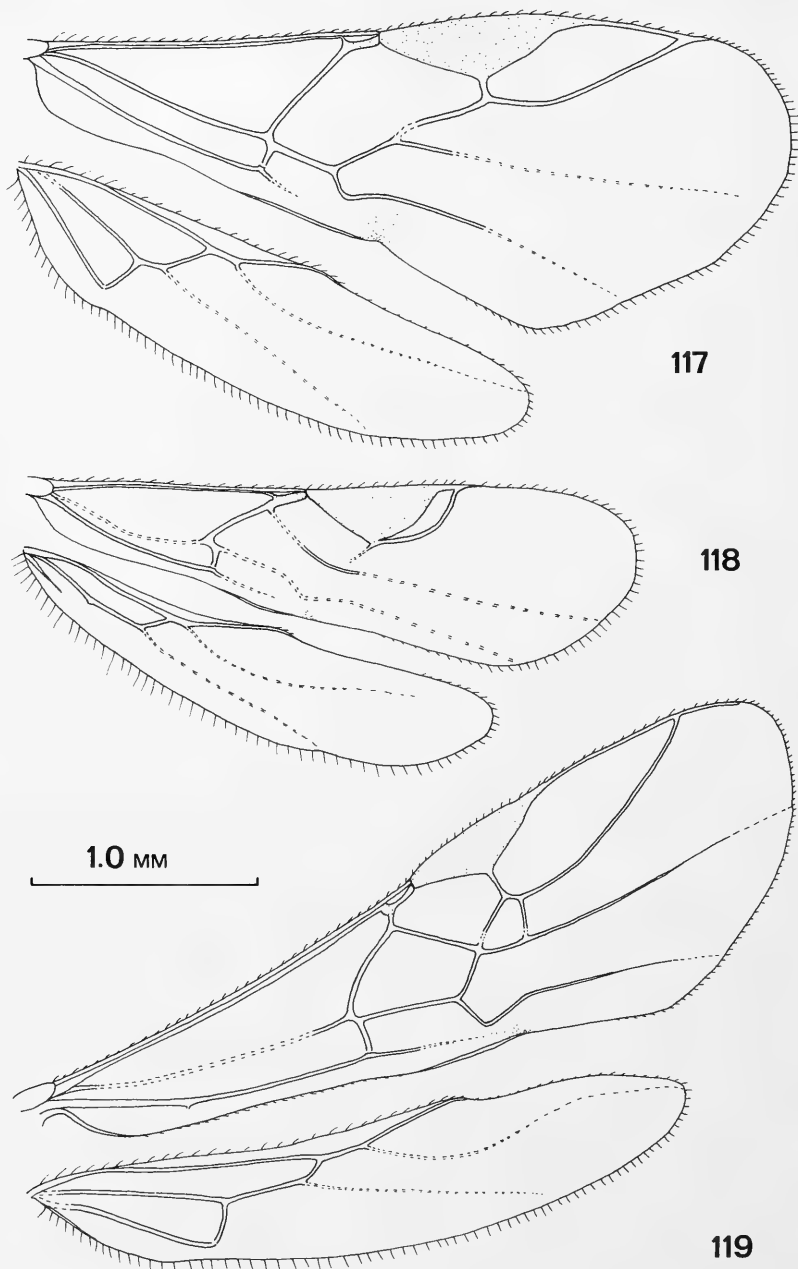


Fig. 117, *Perilitus (Microctonus) cf. deceptor* Wesmael, ♀, Netherlands, Putten (G.); wings. Fig. 118, *Leiophron (Leiophron) apicalis* Haliday, ♀, Netherlands, Oostvoorne; wings. Fig. 119, *Chrysopophthorus spec.*, ♀, Costa Rica, Turrialba; wings. Fig. 117, 118: 1.2 times scale-line; Fig. 119: scale-line

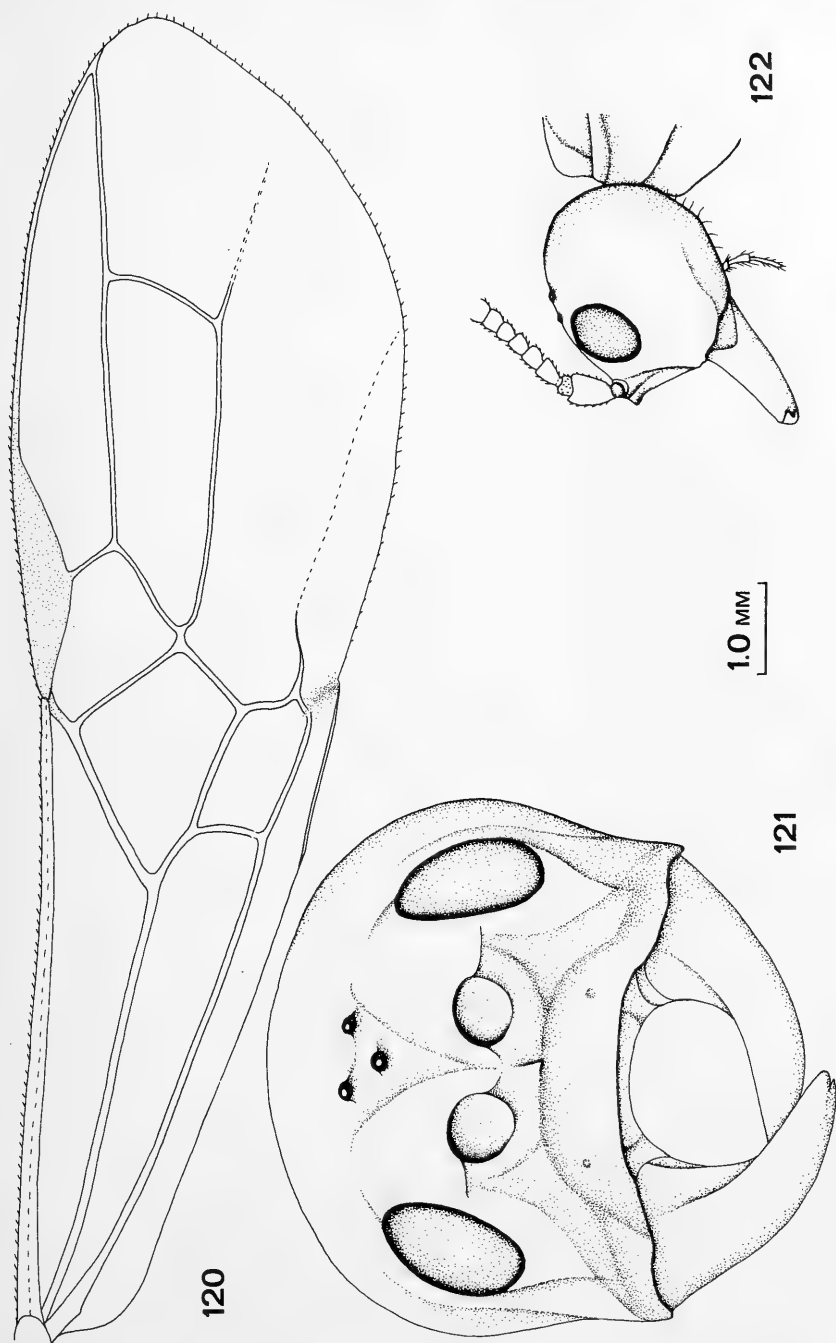


Fig. 120—122, *Pseudodicrogenium monstrosum* Fahringer. 120, fore wing, paralectotype; 121, head, frontal aspect, lectotype; 122, head, lateral aspect, lectotype. Fig. 120, 122: scale-line; Fig. 121: 2.0 times scale-line

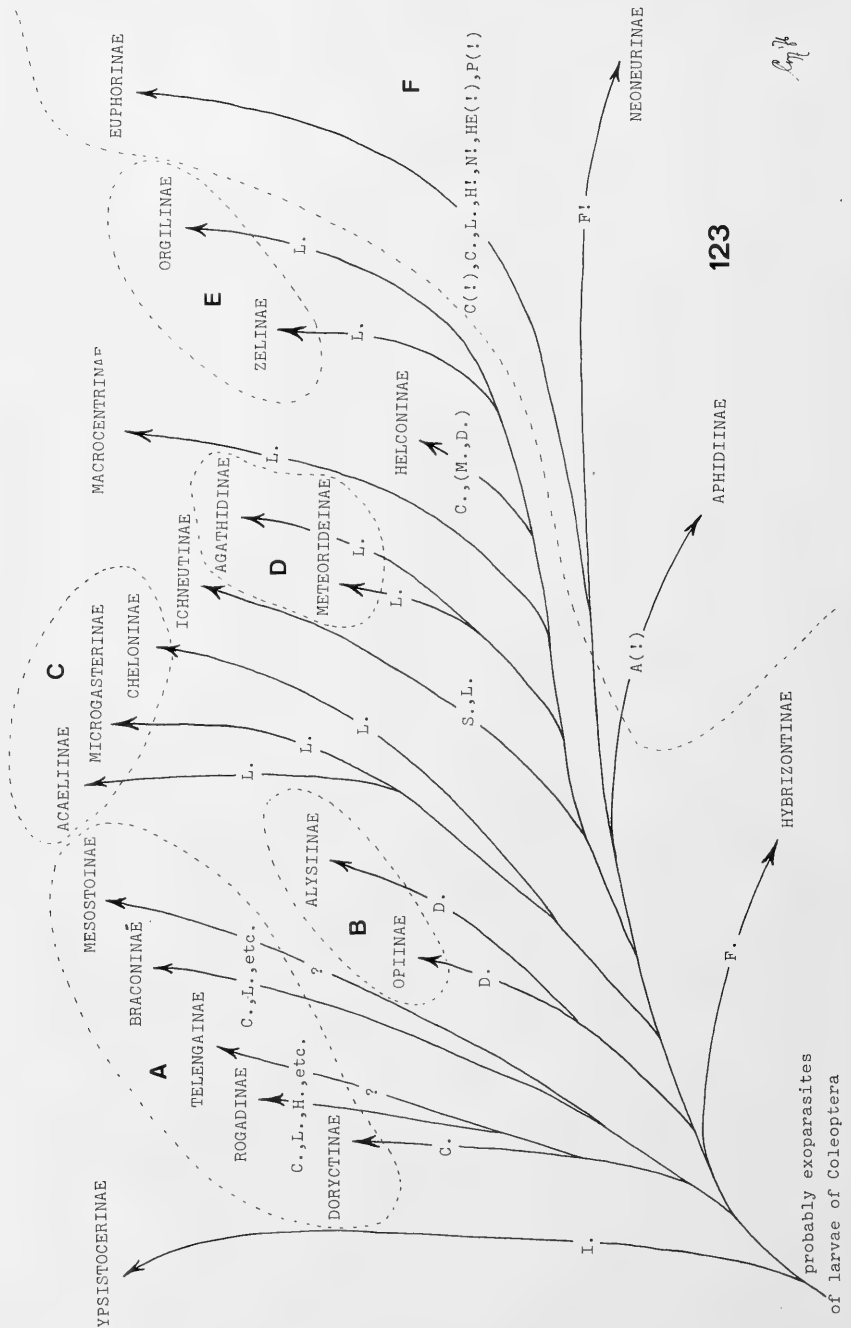


Fig. 123. Dendrogram indicating the possible phylogenetic relationship and the hosts of the subfamilies belonging to the Braconidae. A(!) = parasites of nymphs and adults of aphids; C = parasites of larvae of Coleoptera; C! = parasites of adult Coleoptera; D = parasites of larvae of Diptera; F = parasites of ant-larvae; F! = parasites of adult ants; H = parasites of larvae of Hymenoptera; H! = parasites of adult Hymenoptera; HE(!) = parasites of nymphs and adults of Heteroptera; I = associated with termites; L = parasites of larvae of Lepidoptera; M = parasites of larvae of Mecoptera; N! = parasites of adult Neuroptera; P(!) = parasites of nymphs and adults of Psocoptera; S = parasites of larvae of Symphyta; ? = host unknown







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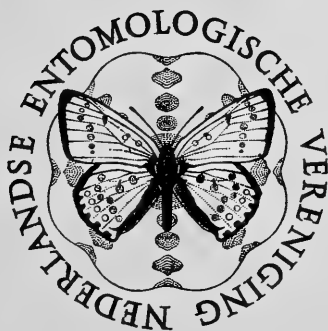
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## INHOUD

J. P. VAN LITH. — New species and records of Indo-Australian Psenini (Hymenoptera, Sphecidae, Pemphredoninae), p. 79—122, fig. 1—53.



# NEW SPECIES AND RECORDS OF INDO-AUSTRALIAN PSENINI (HYMENOPTERA, SPHECIDAE, PEMPHREDONINAE)

by

J. P. VAN LITH

Allard Piersonstraat 28c, Rotterdam

With 53 text-figures

## ABSTRACT

The following new species and subspecies are described and illustrated: *Psen (Psen) nitidus sabahensis*, Sabah, *nitidus binghami*, Sikkim, *elisabethae umboiensis*, New Guinea, *elisabethae bougainvillensis*, Solomon Is., *Psen* (subgenus?) *anodontotus*, New Guinea, *Psen (Mimumesa) oresterus*, West Pakistan, *Psenulus major*, Laos, *decipiens*, Laos, *laosensis*, Laos, *armipes*, Philippine Is., *tectus*, Laos, *anomalous*, Vietnam, *vaneuensis*, Laos, *puncticeps rufipes*, Sumba, *exiguus*, Laos, Malaya, *suturalis*, Laos, *crabroniformis wapiensis*, Laos, *crabroniformis nathani*, South India, *limbatus*, Laos, *impressus*, Philippine Is., *pictus*, New Guinea, *ornatus sumbaensis*, Sumba, *fyanensis*, Vietnam, Laos, *nigrolateralis*, Laos, *vientianensis*, Laos, *leucognathus*, South India. Many new records of known species are given, in some cases also a description of the hitherto unknown opposite sex. *Psen (Mimesa?) inflatus* is transferred to the subgenus *Psen*.

During the past decade, many Psenini have been collected in the Indo-Australian area. Special mention should be made here of the rich material gathered in Laos by native collectors for the Bishop Museum, Honolulu. Thus far no Psenini were known from that country. Now 17 Laotian species and subspecies can be listed, of which 12 are described here as new. Ten of these forms are recorded from Laos only. Much new information has also been obtained with regard to the distribution of earlier described species.

The male genitalia have been figured as much as possible. It is obvious that comparison of the parameres is of good assistance in the classification in species groups or subgenera. Since my last key to the Indo-Australian species of *Psenulus* (1962) the number of forms has more than doubled and now amounts to 134. A new key for *Psenulus* is now in preparation. Notwithstanding the progress made our knowledge of the Indo-Australian Psenini is still very incomplete; much more collecting in this region is highly desirable. Of only 36 forms both sexes are known. For 62 females and for 36 males the opposite sex has not yet been found or recognized. For the genus *Psen* the figures are somewhat better (40, 31 and 18, respectively). We know very little about their bionomics. Best known in this respect is *Psenulus sogatophagus* Pagden, 1933. Dr. D. H. Murphy, Singapore, kindly provided some information regarding nesting and prey of *Psenulus trimaculatus*.

I am much obliged to the Bishop Museum and all other friends and institutions who sent me their material for study. Their names are given below together with the symbols used in the text. Special thanks are due to Prof. J. van der Vecht, who stimulated me long ago to study the Psenini and continues to show interest, and to

Mrs. E. van der Vecht-Bourguignon who collected two new species during their visit to New Guinea in 1972.

- AMNH — The American Museum of Natural History, New York, N.Y., U.S.A.; Mrs. M. Favreau, J. G. Rozen Jr.
- BISH — Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.; Miss A. Manning, F. J. Radovsky
- BM — British Museum (Natural History), Department of Entomology, London, U.K.; L. A. Mound, C. R. Vardy
- CGR — C. G. Roche, Kuala Lumpur, Malaysia
- CNC — Entomology Research Institute, Canada Department of Agriculture, Ottawa, Canada; J. Barron, L. Masner, C. M. Yoshimoto
- ELW — Laboratorium voor Entomologie, Wageningen, The Netherlands; via J. van der Vecht
- HT — H. and M. Townes, American Entomological Institute, Ann Arbor, Michigan, U.S.A.
- MA — Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Afdeling Entomologie, Amsterdam, The Netherlands; J. P. Duffels, W. N. Ellis
- ML — Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; J. van der Vecht
- NMB — Naturhistorisches Museum, Basle, Switzerland; via J. van der Vecht
- UI — University of Idaho, Department of Entomology, Moscow, Idaho, U.S.A.; A. R. Gittins
- US — University of Singapore, Singapore; D. H. Murphy
- USNM — National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; P. D. Hurd, K. V. Krombein, A. S. Menke

**Psen Latreille**

**Subgenus Psen**

**Psen (Psen) emarginatus Van Lith**

Van Lith, 1959: 43—44 (Java); 1968: 101—102 (N. Borneo).

New record from Borneo: 1 ♀ and 1 ♂, Sabah, Mt. Kinabalu, 5000 ft, 1—5 May 1973, K. M. Guichard (CGR).

**Psen (Psen) rufoannulatus Cameron**

Cameron, 1907: 90 (India: Simla).

Van Lith, 1965: 58—60; 1973: 125—126 (Nepal).

New record from Nepal: 1 ♂, Kathmandu, 1300—1400 m, 7—12 May 1960, J. and M. Sedlacek (BISH).

**Psen (Psen) nitidus nitidus Van Lith**

Van Lith, 1959: 28—30 (Java, Bangka, Krakatau, Sri Lanka); 1968: 105—106 (S. India, NE. Sumatra).

First record from Malaya: 1 ♀, Johore, Kr. Pulau, 21 Dec. 1967 (CGR).

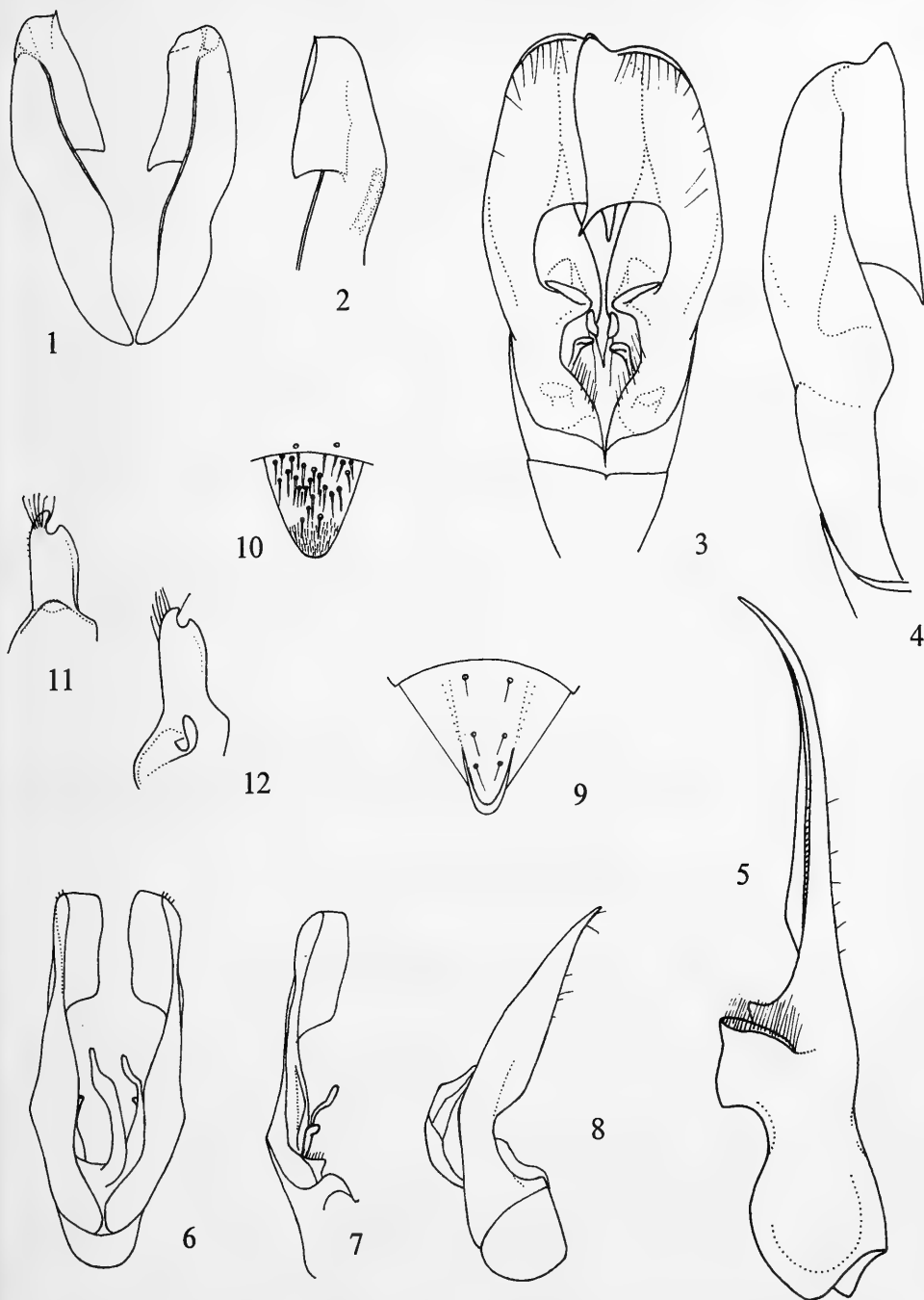


Fig. 1—2. *Psen (Psen) nitidus binghami* subsp. nov., ♂, holotype, outer parts of genitalia, dorsal aspect, paramere, ventral aspect. Fig. 3—4. *Psen (Psen) elisabethae umboiensis* subsp. nov., ♂, holotype, genitalia, ventral and dorsal aspect. Fig. 5. *Psen (Psen) elisabethae bougainvillensis* subsp. nov., ♂, holotype, 8th sternite, lateral aspect. Fig. 6—8. *Psen (Psen) inflatus* Van Lith, ♂, genitalia in dorsal, ventral and lateral aspect. Fig. 9. *Psen anodontotus* sp. nov., pygidial area of ♀, holotype. Fig. 10—12. *Psen (Mimumesa) oresterus* sp. nov., 10, ♀, pygidial area; 11—12, ♂, paramere, outer and inner aspect

***Psen (Psen) nitidus takasago* Tsuneki**

Tsuneki, 1967: 8—9 (Taiwan).

Van Lith, 1968: 106.

New record from Taiwan: 2 ♀, Sauter coll. (AMNH).

***Psen (Psen) nitidus sabahensis* subsp. nov.**

Two females from North Borneo differ from the female of the nominate form and from the female of the subspecies *takasago* in having dark brown instead of yellowish-brown, hind tarsi. The apex of the antennae below is blackish-brown. Fore tibiae and fore and mid tarsi are reddish-brown, slightly darker than in other forms of *P. nitidus*.

Scutum more strongly punctate than in nominate form. Pygidial area broader, its base more shining and punctures along lateral margins larger. Pubescence of scutum somewhat brownish, greyish-white in the nominate form.

Male unknown.

Borneo: 2 ♀, holotype (Roche No. 15222) and paratype (Roche No. 15221), Sabah, Mt. Kinabalu, 5000 ft, 1—5 May 1973, K. M. Guichard (CGR). The holotype has been deposited by Mr. Roche in the British Museum (Natural History), London.

***Psen (Psen) nitidus binghami* subsp. nov.**

Male. — Resembling nominate form but differing in having dark brown hind tarsi, brown mid tarsi, strongly punctate scutum and brownish pubescence on thorax and gaster.

Genitalia (Fig. 1, 2) as in nominate subspecies.

Sikkim: 1 ♂, holotype, coll. Bingham 1902—120 (BM).

***Psen (Psen) elisabethae elisabethae* Van Lith**

Van Lith, 1959: 31—34 (Java, Sumatra); 1968: 106 (Vietnam).

New record from North Sumatra: 1 ♀, Sibolangit, Lörtzing (ELW ex coll. Roepke).

New record from West Java: 1 ♂, Mt. Gedeh, 14 Aug. 1965, J. E. Lukavsky (CNC).

***Psen (Psen) elisabethae madrasiensis* Van Lith**

Van Lith, 1968: 107 (S. India).

First records from Laos: Vientiane Prov., Ban Van Eue, 1 ♀, 15 Febr. 1966, Malaise trap, 1 ♂, 29 March 1966, native collector (BISH).

The face of this female is distinctly silvery pubescent. Pygidial area narrow, as in nominate subspecies.



***Psen (Psen) elisabethae umboiensis* subsp. nov.**

Male. — Much resembling nominate form. Length about 10 mm. Femora and tibiae black, tarsi yellowish-brown, antennae and tegulae black. Petiole about twice as long as first tergite. Last antennal segment over twice as long as broad at base. Pubescence of face and tempora silvery-white, mostly appressed. Pubescence of rest of body whitish, thorax dorsally more greyish. Genitalia (Fig. 3, 4) large, brown.

NE. New Guinea: 1 ♂, holotype, Umboi I., about 8 km WNW. of Lab Lab, 300 m, 8—19 Febr. 1967, G. A. Samuelson, Malaise trap; 1 ♂, paratype, Umboi I., 1 km N. Awelkom, 600 m, 21—28 Febr. 1967, G. A. Samuelson, Malaise trap (BISH).

This subspecies is distinguished from the nominate form by the larger size, longer antennae and dark legs and tegulae.

***Psen (Psen) elisabethae bougainvillensis* subsp. nov.**

Male (holotype). — Resembling preceding form. Length over 11 mm. Legs and tegulae black, tarsi yellowish-brown. Petiole about 1½ times as long as first tergite. Last antennal segment over 2½ times as long as broad at base. Punctuation fine. Pubescence as in preceding form. Eighth sternite: Fig. 5.

Solomon Is.: 1 ♂, holotype, Bougainville, Kukugai Vill., 150 m, Nov. 1960, W. W. Brandt (BISH).

The genitalia of this specimen are like those of the subspecies *umboiensis*. It is distinguished from the nominate subspecies by the dark legs, shorter petiole, longer antennae and large size. It differs from *umboiensis* by the shorter petiole and longer antennae.

***Psen (Psen) coriaceus* Van Lith**

Van Lith, 1959: 34—36 (Mindoro, Luzon, Negros, Mindanao).

New record from Luzon: 1 ♀, Baguio, June 1917, F. X. Williams (BISH).

***Psen (Psen) paulus paulus* Van Lith**

Van Lith, 1968: 113—114 (New Guinea).

New records from NE. New Guinea: 1 ♀, Mt. Missim, 980 m, Malaise trap, 20 July 1969, J. L. Gressitt and Y. Hirashima, 1 ♂, Mt. Missim, 1300 m, Malaise trap, 7—21 Dec. 1966, G. A. Samuelson, 2 ♂, Wau, 1000 m, 23 Dec. 1969, M. Sedlacek (BISH).

SE. New Guinea: 1 ♂, Mamai Pltn, E. of Port Glasgow, 150 m, light trap, 17 Febr. 1965, R. Straatman (BISH).

***Psen (Psen) bryani* Perkins & Cheesman**

Perkins & Cheesman, 1928: 28—29 (Samoa).

Van Lith, 1968: 116.

New records from Samoa: 1 ♀, Tutuila I., 9 Aug. 1957, W. R. Kellen, 2 ♂, Tutuila, Vatia, 0—200 m, 9 March 1971, N. L. H. Krauss (BISH).

### ***Psen (Psen) hakusanus seminitidus* Van Lith**

Gussakovskij, 1934: 7 (*Mimesa kohli*, nec *Psen kohli* Fox, 1898; China); 1937: 653 (*Psen kohli*; China, Tibet).

Van Lith, 1965: 40 (*Psen (Psen) seminitidus* new name); 1968: 119.

Tsuneki, 1966: 9—10 (*Psen (Psen) hakusanus seminitidus* new status; Taiwan); 1967: 2—3; 1971: 17.

New record from Taiwan: 1 ♀, Taiwan C., Alisan, 2400 m, 3—9 July 1972, T. C. Maa (BISH).

### ***Psen (Psen) orientalis* Cameron**

Cameron, 1890: 269 (Madras, India); 1902: 289 (*Psen reticulatus*; India).

Van Lith, 1965: 42—44; 1968: 120—121.

New record from Kashmir: 1 ♀, Gulmarg, summer 1913, F. W. Thomson (BM).

### ***Psen (Psen) politiventris politiventris* Rohwer**

Rohwer, 1921: 321 (*Psen (Mimesa) politiventris*; Luzon).

Van Lith, 1959: 36—37 (*Psen (Psen) politiventris*); 1965: 48.

New records from Luzon: Mountain Prov., Abatan, Buguias, 60 km S. of Bontoc, 1800—2000 m, 1 ♂, 27 May 1964, 1 ♀, 15 June 1964, H. M. Torrevillas (BISH).

### ***Psen (Psen) alishanus* Tsuneki**

Tsuneki, 1967: 3—5 (Taiwan); 1971: 1, 17.

New records from Taiwan: 2 ♀, Taiwan C., Alisan, 2400 m, 3—9 July 1972, T. C. Maa (BISH).

### ***Psen (Psen) refractus meridianus* Van Lith**

Van Lith, 1965: 51—52 (S. India).

New record from South India: 1 ♀, Anamalai Hills, Cinchona, 3500 ft, May 1969, P. S. Nathan (MA).

### ***Psen (Psen) aureohirtus aureohirtus* Rohwer**

Rohwer, 1921: 322—323 (*Psen (Mimesa) aureohirta*; Philippine Is.).

Van Lith, 1959: 49—50 (*Psen (Psen) aureohirtus*); 1965: 56; 1968: 121.

New record from Luzon: 1 ♀, Mountain Prov., Abatan, Buguias, 60 km S. of Bontoc, 1800—2000 m, 9 May 1964, H. M. Torrevillas (BISH).

***Psen (Psen) ruficrus* Van Lith**

Van Lith, 1965: 62—63 (New Guinea); 1968: 122—124.

New records from NE. New Guinea: 30 km E. of Goroka, 2000—2100 m, 1 ♀, 15—21 April 1968, 1 ♂, 22—31 May 1968, J. and M. Sedlacek (BISH).

***Psen (Psen) sedlaceki* Van Lith**

Van Lith, 1968: 124—125 (New Guinea).

New record from NE. New Guinea: 1 ♂, Morobe District, Ulap, 800—1100 m, Sept. 1968, N. L. H. Krauss (BISH). This is the second male recorded, the female is still unknown.

***Psen (Psen) inflatus* Van Lith**

Van Lith, 1968: 129—130, ♀ (*Psen (Mimesa?) inflatus*; Central New Guinea).

New records: NE. New Guinea, Wau, 1 ♂, Jan. 1970, 1 ♀, 2100—2300 m, 3 Aug. 1971, Sedlacek (BISH); 2 ♂, Wau, 2100—2360 m, Mt. Kaindi, 14 Sept. 1972, J. van der Vecht (ML).

Female. — Somewhat darker than the form from Central New Guinea. Head, scutum and mesopleura including hypo-epimeral area black, with indistinct bluish-black shine, propodeum with steel-blue or violet-blue reflections. Dorsum and ventral plate of petiole black, sides and underside of petiole dark reddish-brown. Gaster black with metallic-blue shine, apex reddish-brown. Femora with light metallic shine, hind tibiae dorsally dark brown, reddish-brown below. Apical third of fore wings infusate. Interantennal tooth blunt in dorsal aspect, as in the females from Central New Guinea. Petiole about ten times as long as wide in the middle, in dorsal aspect.

First description of male. — Resembling female. Scape and following segment of antennae and basal half of underside of flagellum reddish. In two of the males the epicnemium has a violet-blue metallic shine, in one of these two males the mesopleura including hypo-epimeral area with the same shine. The male caught in January has a completely brownish-black petiole, in the two other males the petiole is reddish-brown with dark dorsal line.

Antennae long, third segment about four times, segments 4—6 over 2½ times, segments 7—10 about 2½ times, segments 11—12 over twice as long as broad at apex, segment 13 over 2½ times as long as broad at base. No tyloidea. Gastral sternites 3—4 with long, dark brown fasciculate hairs in middle of hind margin. Genitalia (Fig. 6—8) long, brownish-yellow, inner apex of stipes with long and broad membranous extension or flag.

Because of the characteristic fasciculate hairs on sternites 3—4 of the male and the structure of the genitalia this species has now been placed in the subgenus *Psen*, although the epicnemial region in some respects more resembles that of *Mimumesa*. The cone-shaped, laterally extending hypo-epimeral areas and the high transverse carinae on the ventral side of the thorax distinguish this form from any other species of *Psen* s.l.

The specimens from NE. New Guinea differ from the two females from Central New Guinea mainly in the metallic shine of the propodeum not being bronze or brassy, but steel-blue or violet-blue. There are no distinct structural differences. The north-eastern form may represent a different subspecies. The metallic reflection varying in intensity and also the colour of the petiole being variable in the males, a decision must be postponed until more material, especially from Central New Guinea, is available.

***Psen* (?*Psen*) *anodontotus* sp. nov.**

Female (holotype). — Head and thorax shining black, sides and back of thorax with some steel-blue shine. Labrum and median part of mandibles dark reddish, palpi pale brown, pronotal tubercles dark brown, tegulae reddish-brown. Apex of scape of antennae below and flagellum below brownish. Femora dark brown, reddish on foreside, also fore trochanters reddish. All tibiae and tarsi reddish, except fore and mid basitarsi which are pale yellowish. Petiole black, apex dorsally and ventral plate and rest of gaster reddish. Veins of wings black.

Frons impunctate and shining, on both sides of median carina somewhat convex; vertex shining with a few punctures. Back of head more densely punctate. Frontal carina very slightly broadening downwards, not ending in a tooth between antennae. Clypeus densely finely punctate, apical margin shining, very slightly emarginate, almost blunt, basal half of disk convex. Occipital carina below rather high, ending normally in hypostomal carina. Scape long and slender, about five times as long as broad, flagellum clavate, third segment about  $3\frac{1}{2}$  times, fourth segment about twice as long as broad at apex, following segments gradually thickening, segments 8—11 as long as broad or slightly less, segment 12 about  $1\frac{1}{2}$  times as long as broad at base. Mandibles bidentate at apex.

Dorsum of pronotum narrow, lateral corners sharp. Scutum and scutellum shining, sparsely but distinctly punctate, metanotum finely punctate. Dorsal and hind part of propodeum forming a distinct angle. Enclosed area of propodeum triangular, median two longitudinal carinae much diverging, lateral parts with only a few oblique carinae. Behind propodeal enclosure a broad smooth and shining area, back of propodeum with coarse reticulate carination, sides almost smooth. Metapleura shining. Mesopleura and mesosternum shining with a few fine punctures. Hypo-epimeral area strongly convex, smooth and shining. Anterior oblique suture foveolate, surface of anterior plate dull. Interepicnemial area roundly depressed, depression margined laterally by a distinct carina, which continues into the inner carina of the epicnemial areas; at the junction of these carinae a short backwards bent carina defining inner third of lower part of epicnemial area. Outer epicnemial carina slightly bent backwards, epicnemial areas not closed below. Acetabular carina a little behind the carina margining the interepicnemial area, slightly longer than half the distance between outer epicnemial carinae. Behind acetabular carina a few weak transverse carinae, median mesosternal carina distinct, ending before apex. Metasternum emarginate (angle about 135 degrees), with transparent margin. Legs rather thick. Upper two-thirds of back of hind femora smooth and shining, separated from lower part,

which bears a few hairs, by a narrow dull stripe consisting of very fine punctures, each bearing a short fine hair. Second recurrent vein of fore wings ending just in third submarginal cell.

Petiole cylindrical, slender, about  $1\frac{1}{2}$  times as long as first tergite, dorsally smooth. Gaster shining, hardly punctate, broad hind margins of tergites smooth, impunctate. Pygidial area (Fig. 9) shining, elongate-triangular, apex rounded, lateral carinae distinct but short, along margin a few punctures.

Head and thorax whitish pubescent, pubescence on clypeus silvery, mostly short and appressed, near apex of clypeus a few long stiff yellowish hairs. Tempora somewhat appressed whitish pubescent. Petiole ventro-laterally with fine and long, obliquely downward directed hairs. Pubescence of legs yellowish-golden, on gaster sparse, denser on sixth sternite.

Length about 7.5 mm.

Male unknown.

East New Guinea: 1 ♀, holotype, Wau, 1500 m, McAdam Park, on *Hibiscus* flowers, 17 Sept. 1972, Mrs. E. van der Vecht (ML).

*P. anodontotus* differs from the other species of the subgenus *Psen*, where it is provisionally placed, in having short, clavate antennae, in the interepicnemial area which is depressed and margined below by a fine rounded carina in front of the acetabular carina, and by the inner carinae of the epicnemial areas. The inter-antennal carina does not end in a sharp tooth or elevated area, as is usual in the subgenus *Psen*. The structure of the epicnemial region is similar to that of the palaearctic species of the subgenus *Mimumesa* Malloch. The petiole differs, however, in being cylindrical instead of carinate.

### Subgenus *Mimumesa* Malloch

#### *Psen* (*Mimumesa*) *oresterus* sp. nov.

Female. — Length about 6.5 mm. Rather resembling the palaearctic *P. littoralis* (Bondroit). Apical three antennal segments pale brown, rest of underside of antennae dark brown. Tarsi brown, tarsal segments 2—5 of fore legs pale brown.

Punctuation of head between ocelli and oculi as in *P. littoralis*, vertex with some fine transverse striation. Scutum shining, distinctly finely punctate, hind margin with short longitudinal striae; scutellum punctate, posteriorly hardly striate. Metanotum dull. Central area of propodeal enclosure without median longitudinal carina (holotype) or with irregular median longitudinal carina (paratype). Pygidial area (Fig. 10) as in *P. littoralis*.

Male. — Same size. Rather resembling *P. unicolor* Van der Linden, but vertex not densely punctate. Antennae brown below, apical three segments paler. All tarsi and apex of fore tibiae pale brown.

Antennal segments 4—12 with linear tyloidea, tyloides on segment 12 about  $\frac{2}{3}$  of total length of segment and situated on basal half. Scutellum posteriorly slightly striato-punctate. Central area of propodeal enclosure with median longitudinal carina. Genitalia: Fig. 11, 12.

West Pakistan: Quetta, Baluchistan, 2 ♀, holotype and paratype, 1 ♂, allotype, June 1902, 1 ♂, paratype, Aug. 1903, C. G. Nurse (BM).

The last mentioned male has a deformed petiole, with apex about half as broad as propodeum and about twice as long as it is wide at apex.

### Subgenus *Mimumesa*?

#### *Psen* (*Mimumesa*?) *tridentatus tridentatus* Van Lith

Van Lith, 1959: 55—56 (Sumatra); 1965: 67 (Malaya).

First record from Vietnam: 1 ♀, 17 km S. of Dilinh, 1300 m, 6—13 Oct. 1960, C.M. Yoshimoto (BISH).

First record from Laos: 1 ♂, Vientiane Prov., Ban Van Eue, 29 March 1966, native collector (BISH).

The genitalia of this male agree with those of a male of *P. tridentatus chrysomallus* from Burma. Basiparameres and parameres chestnut brown, valves of aedeagus (Fig. 15) yellowish-brown, volsellae dark brown. Basiparameres and parameres (Fig. 13, 14) heavily built, parameres thick, inner margin with fringe of stiff hairs.

The subgeneric position of *P. tridentatus*, *P. auratus* and *P. multipunctatus* is still uncertain. Their genitalia are very similar to those of *Mimumesa*, in which subgenus they were originally placed, but they are much heavier. They are much different from the genitalia of the subgenera *Psen*, *Punctipsen* and *Pseneo*. The petiole is remarkable because of the structure of the dorsal side. It has an irregular apical groove and large lateral punctures prolonged into short grooves. The propodeum is conspicuously longitudinally striate. The acetabular carina is complete, as in *Mimumesa* and *Pseneo*. In *P. tridentatus* the clypeal margin is more or less tridentate. Although in *Pseneo* the acetabular carina, clypeal margin and pygidial area are very similar and the sternal apical tufts are equally lacking in the

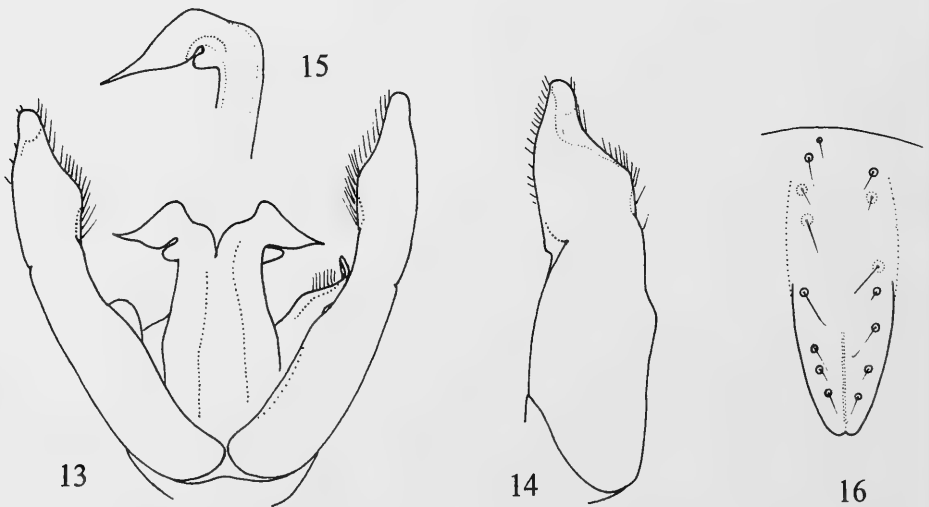


Fig. 13—15. *Psen tridentatus tridentatus* Van Lith, ♂, 13—14, genitalia in dorsal and lateral aspect; 15, penis valve. Fig. 16. *Psen tridentatus chrysomallus* Van Lith, ♀, pygidial area

males, I do not believe that *P. tridentatus* should be considered to belong to this genus. Probably a new subgenus should be erected for the three species in question. This subgenus would mainly be characterized by the structure of propodeum and petiole, the complete acetabular carina and the lack of sternal tufts. I hope to return to this problem later.

***Psen (Mimumesa?) tridentatus chrysomallus* Van Lith**

Van Lith, 1965: 68, ♂ (Burma).

Fortunately also the female of this subspecies has turned up. It was collected a few days earlier than the two males described in 1965, at the same locality.

It resembles the female of the nominate form, but is distinguished by the larger size, the paler base of the antennae and the stronger sculpture of scutum and propodeum.

Anterior margin of clypeus as in male (Van Lith, 1965: Fig. 77). Frons below median ocellus with two small low tubercles, each at a distance from median ocellus and from median frontal carina about as large as diameter of ocellus. A slightly raised elongate smooth area along oculi. Vertex not densely, partly very finely, punctate. Third antennal segment in frontal view about four times as long as broad at apex, following two segments about twice, sixth segment about  $1\frac{1}{2}$  times as long as broad, segments gradually diminishing in length, segment 11 about as long as broad at apex and last segment about  $1\frac{1}{2}$  times as long as broad at base.

Scutum more closely punctate than in nominate form, especially in the middle of the scutum, with only a few small interstices between the punctures. In the nominate form the smooth spaces between the punctures are much larger in the middle of the scutum, about four or five times as large as diameter of punctures. Anterior margin of scutum much finer punctate in both forms, but in the female from Burma distinctly finer than in the nominate form. Enclosed area of propodeum not depressed, behind this area the number of longitudinal carinae is greater than in the nominate form, as a consequence the smooth areas in the antero-lateral corners of the back of the propodeum are smaller. Punctuation of tergites fine and rather dense, interstices on apical half about three or four times as large as punctures, interstices on margin of tergites 4—5 larger. The fine punctures on the fifth tergite are intermixed with a few larger punctures, it has a broad smooth margin. Petiole as in nominate form. Pygidial area also similar, lateral keels high, apex with small emargination, apically an indistinct median longitudinal keel (Fig. 16).

Face with dense, appressed silvery pubescence and also with long silvery hairs. Pubescence of gaster paler than in male. Apical margin of first two tergites with a row of long, sideways directed, pale golden hairs. The hairs should be examined from above, because they may appear to be much darker when seen from aside. Apical margin of first two tergites laterally and margins of tergites 3—4 with long whitish hairs, also pubescence on disk of all tergites very pale.

Length about 13 mm.

Upper Burma: 1 ♀, Nam Tamai Valley, 3000 ft, lat: N 27°42', long. E 97°54', 12 Aug. 1938, R. Kaulback (BM).

***Psen (Mimumesa?) multipunctatus* Van Lith**

Van Lith, 1959: 55 (Negros); 1965: 68 (*Psen (Mimumesa) auratus multipunctatus*; Luzon).

New record from Negros: 1 ♀, Negros Or., L. Balisasayao, 1—7 Oct. 1959, L. W. Quate (BISH).

New record from Luzon: 1 ♀, Mount Prov., Ifugao, Mayoyao, 1000—1500 m, 11 July 1966, H. M. Torrevillas (BISH).

Because of the strong punctuation of the gaster this form is now recognized as a distinct species. The male is still unknown.

***Psenulus Kohl*  
*Psenulus bicinctus* Turner**

Turner, 1912b: 363—364 (Assam).

Van Lith, 1972: 159—160 (Assam, Sikkim, Nepal).

First record from Burma: 4 ♂, NE. Burma, Kambaiti, 7000 ft, 1 May 1934, R. Malaise (BM).

Apparently the colour of the gaster is somewhat variable. In two of the males the first tergite is reddish, the two other males have this tergite largely brownish or blackish. Third tergite with dark brown median area only, fourth tergite dark brown with reddish apical margin.

Petiole nearly twice as long as first tergite, longer than in the female, where it is at most 1½ times as long as first tergite.

Genitalia (Fig. 17) pale yellowish-brown, parameres deeply emarginate on inner side, a triangular tooth on apex of inner side of basiparameres.

***Psenulus orinus* Van Lith**

Van Lith, 1973: 131—133 (Nepal).

New record from Nepal: 1 ♀, Bokaihunde, 20 km N. of Trisuli (Nawakot), 2100 m, 13—17 Nov. 1965, L. W. Quate (BISH).

The genitalia closely resemble those of the preceding species. Both species are placed in the group of *Psenulus rufobalteatus* Cameron. The genitalia of *rufobalteatus* have not yet been examined.

***Psenulus major* sp. nov.**

Male. — Length about 10—10.75 mm. Black, with bluish shine. Base of flagellum below, base of mandibles, labrum, palpi and fore tibiae and tarsi reddish-brown; mid tarsi, base of hind tibiae, tegulae, apex of petiole and sides of first tergite brown. Wings distinctly fuscate, veins brown.

Interantennal carina sharp, ending below antennae in a low transverse carina. Clypeus shining, densely superficially punctate, anterior margin with deep, almost triangular emargination and short lateral teeth. Frons densely minutely punctate, vertex shining, sparsely finely punctate, tempora densely very finely punctate.



Antennae long, segments rounded below, about twice as long as broad at apex or  $1\frac{1}{2}$  times as long as broad in the middle. Segments 4—12 with narrow tyloidea, on most segments almost as long as segment, indistinct carina on segment 3. Occipital carina ending in hypostomal carina.

Lateral corners of pronotum obtuse. Scutum shining, distinctly punctate, interstices up to a few times size of punctures, sometimes in rows, punctures much finer and sparser on outer side of subpleural sutures. Prescutal sutures distinct, reaching hind margin. Scutellum shining, distinctly punctate, much sparser on anterior half. Enclosed area of propodeum triangular, shining; central area wide, with indistinct median carina, in lower part with a few transverse arched carinae. Back of propodeum coarsely reticulate, carinae almost parallel on upper part, horizontal part behind enclosed area smooth and shining. Mesopleura, hypopleural area, mesosternum and anterior plate of mesepisternum shining, sparsely finely punctate. Anterior oblique suture foveolate, widened upper part with longitudinal carinae. Legs slender. Petiole almost cylindrical, about twice as long as first tergite, apex above with short, elongate-triangular groove. Gastral segments shining, densely finely punctate. Eighth gastral sternite with long spine.

Genitalia (Fig. 18) dark brown, parameres broad with rounded apex, apex of basiparameres on inner side with large triangular tooth.

Pubescence of face and frons greyish-brown, dense and short, with some longer hairs, laterally somewhat depressed but not on clypeal disk so that the sculpture is easily seen. Thorax and gaster brownish-grey pubescent, mesosternum whitish. Petiole latero-dorsally with a row of mostly short hairs, latero-ventrally with long erect hairs, ventral plate with dense short pubescence.

Laos: 1♂, holotype, Vientiane Prov., Ban Van Eue, 29 March 1966; 6♂, 15 March 1966, 3♂, 29 March 1966, 1♂, 30 March 1966, 1♂, 30 March 1967, all paratypes, same locality, some specimens collected in Malaise trap, native collectors (BISH).

The punctuation of the scutum varies somewhat and is in some paratypes finer and sparser than in the holotype.

*P. major* is easily distinguished from other black *Psenulus* by the narrow interantennal carina, the long and narrow tyloidea, large size and long petiole.

### ***Psenulus decipiens* sp. nov.**

Male (holotype). — Length about 8 mm. Head and thorax black. Mandibles except tips yellowish-red, palpi yellowish-brown. Scape of antennae and underside of flagellum yellowish-brown, flagellum dorsally brown. Pronotal tubercles brown. Legs including trochanters yellowish-red, fore and mid femora below somewhat brown. Gaster including petiole yellowish-red. Veins of wings dark brown.

Anterior margin of clypeus bidentate, distinctly emarginate. Interantennal carina narrow, ending below antennae in transverse carina. Frons and vertex sparsely finely punctate. Postocellar area not raised. Occipital carina ending before hypostomal carina. Antennae about as long as head and thorax together, segments rounded below, segment 3 about  $2\frac{1}{2}$  times, segments 4—12 about twice

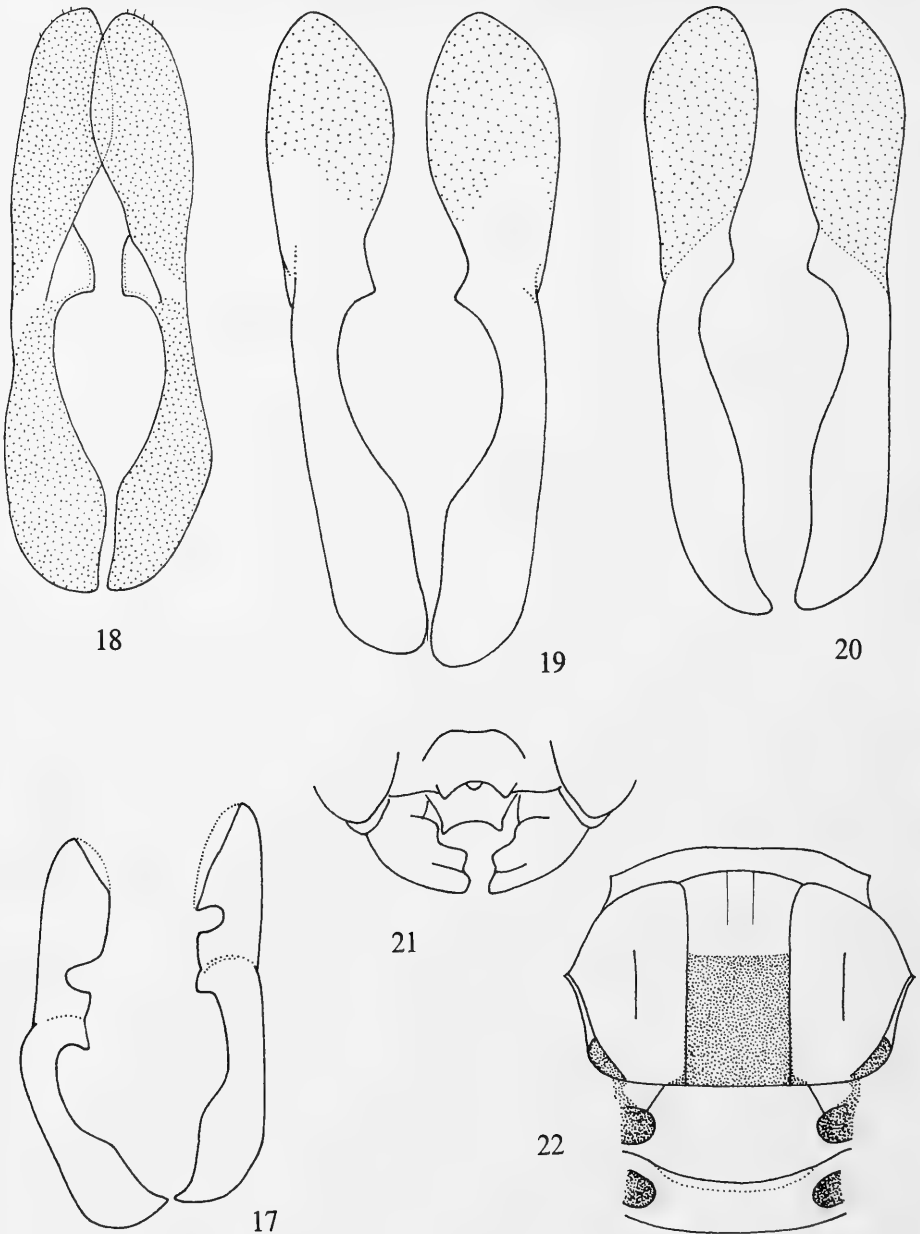


Fig. 17—20. Male basiparameres and parameres, dorsal aspect, of various species of *Psenulus*. 17, *P. bicinctus* Turner, Burma; 18, *P. major* sp. nov., paratype; 19, *P. decipiens* sp. nov., holotype; 20, *P. laosensis* sp. nov., paratype. Fig. 21—22. *Psenulus armipes* sp. nov., ♀, holotype, 21, face, lower part; 22, thorax, dorsal aspect

as long as broad at apex, last segment over  $2\frac{1}{2}$  times as long as broad at base. No distinct tyloidea.

Pronotal corners rounded. Scutum shining, distinctly irregularly punctate, on anterior half weaker and more sparsely. Prescutal sutures as long as scutum, less distinct on posterior half. Scutellum and metanotum shining, sparsely punctate. Enclosed area of propodeum narrow, longitudinal groove narrow, back of propodeum shining, below and laterally irregularly carinate, also posterior half of sides. Mesopleura, hypo-epimeral area, anterior plate of mesepisternum and mesosternum shining, minutely punctate. Anterior oblique suture foveolate, widened upper part with a few oblique carinae. Legs slender. First recurrent vein of fore wings ending well before end of first submarginal cell. Petiole cylindrical, little longer than first tergite, apex with small triangular groove. Gastral tergites minutely sparsely punctate.

Pubescence of face and dorsal side of pronotum silvery, mostly appressed. Pubescence of rest of body yellowish-grey.

Genitalia (Fig. 19) resembling those of *P. laosensis*, basal part yellowish-brown, greater part of parameres dark brown, apex rounded, inner corner of basiparameres with low tooth.

Laos: 1♂, holotype, Vientiane Prov., Ban Van Eue, 15—31 May 1965, native collector (BISH).

*P. decipiens* seems to be closely related to *P. major* and *P. laosensis* but differs, besides in other characteristics, in the absence of distinct tyloidea.

### ***Psenulus laosensis* sp. nov.**

Male. — Length about 8 mm. Head and thorax black; mandibles except apices yellowish, palpi brownish-yellow, antennae dark brown, scape and basal half of underside of flagellum reddish-brown, pronotal tubercles yellowish-brown. Legs including trochanters and gaster including petiole yellowish-red. Veins of wings brown.

Anterior margin of clypeus bidentate, distinctly emarginate. Interantennal carina very slightly broadened dorsally, with fine groove, carina ending below antennae in transverse carina. Occipital carina ending before hypostomal carina. Frons and vertex minutely sparsely punctate. Postocellar area not raised. Antennae longer than head and thorax together, segments laterally somewhat flattened, underside rounded. Segment 3 in lateral view over twice, segments 4—10 about twice, segments 11—12 over twice as long as broad at apex, segment 13 nearly three times as long as broad at base. Segments 4—12 with oblique long narrow tyloidea, longest on median segments but not reaching base or apex.

Pronotal corners rounded. Scutum shining, minutely punctate, prescutal sutures distinct on anterior half, less distinct on posterior half. Scutellum and metanotum shining. Enclosed area of propodeum short triangular; upper part of back of propodeum shining, lower part and posterior part of sides reticulate, median longitudinal groove narrow. Mesopleura, hypo-epimeral area, anterior plate of mesepisternum and mesosternum shining, indistinctly punctate. Anterior oblique suture foveolate, widened upper part with a few oblique carinae. Legs slender.

First recurrent vein of fore wings ending in second submarginal cell. Petiole almost cylindrical, nearly  $1\frac{1}{2}$  times as long as first tergite, a small triangular depression at apex. Gastral tergites minutely punctate.

Basal part of genitalia (Fig. 20) reddish-brown, parameres dark brown, broad with rounded apex, inner shoulder of basi-parameres with low tooth.

Pubescence of face and pronotum pale golden, mostly appressed, of rest of body yellowish-brown.

Laos: 1♂, holotype, Vientiane Prov., Ban Van Eue, 29 March 1966, native collector; 4♂, paratypes, same locality, 15—30 March 1966, one in Malaise trap, native collector (BISH).

*P. laosensis* is probably closely related to the entirely black *P. major*, perhaps also to *P. decipiens*.

### ***Psenulus armipes* sp. nov.**

Female (holotype). — Length about 8 mm. Head black; basal half of mandibles yellow, palpi straw-yellow. Scape of antennae yellowish, following segments dorsally brown, ventrally yellowish-brown. Thorax yellow, lower part of pronotum black, propleura dark brown. Posterior  $\frac{3}{5}$  of area between prescutal sutures black, posterior corners of scutum black (Fig. 22). Metapleura and an adjacent mark on mesopleura brown, a brown streak on mesopleura below. Interepicnemial area and median longitudinal band on mesosternum brown. Enclosed area of propodeum, median longitudinal groove and narrow apical margin of propodeum black. Fore and mid legs including coxae yellow, hind legs yellowish-red, hind coxae yellowish. Petiole dark brown, ventral plate of petiole and gaster reddish.

Head thick. Frontal carina raised and widened between antennae, broadened part about twice as long as broad, ending below antennae in a short, arched, transverse carina. Clypeus flat, superficially finely punctate, median part of anterior margin raised, widely emarginate, lateral teeth large and protruding in lateral view. In frontal view a median tooth on a lower level is visible (Fig. 21). Frons shining, depressed medially. Vertex shining, finely punctate, a deep oblique groove along lateral ocelli. Occipital carina ending in hypostomal carina. Mandibles with tooth near upper base, apex bidentate, lower teeth blunt (worn off?). Fore margin of labium blunt, laterally with tooth. Antennae short, clavate, third segment about three times as long as broad at apex, following segments gradually decreasing in length, segments 9—11 about as long as broad at apex, last segment about  $1\frac{1}{2}$  times as long as broad at base.

Pronotal angles with small tooth. Scutum shining, prescutal sutures sharp and narrow, reaching hind margin of scutum, apically slightly widened and deeper. Enclosed area of propodeum triangular with distinct median carina, lateral carinae oblique. Back of propodeum smooth, longitudinal groove narrow. Anterior oblique suture narrow, widened upper part smooth. Legs rather thick, base of hind tibiae flattened and with thin spine about twice as long as width of base of tibia. On outer side of hind tibiae a few stout reddish thorns. Petiole about  $1\frac{1}{2}$  times as long as first tergite, cylindrical, flattened dorsally, base with lateral ridge. Pygidial area elongate-triangular, apex rounded.

Face with silvery, mostly appressed, pubescence, rest of body yellowish-grey pubescent, pubescence on mesosternum and sixth sternite more dense and golden. Petiole laterally with long erect hairs.

Male unknown.

Philippine Is.: 1 ♀, holotype, Misamis Or., Dinawihan Gingoog, 26 km E. of Gingoog City, 100—300 m, 15 August 1965, H.M. Torre Villas, Malaise trap (BISH).

*P. armipes* belongs to the group of *P. scutatus*. It differs from *P. scutatus* in colour as well as in the shape of the clypeal margin.

### ***Psenulus tectus* sp. nov.**

Female (holotype). — Length about 8.5 mm. Head black, margin of clypeus somewhat reddish transparent. Basal  $\frac{3}{5}$  of mandibles yellow, apex dark reddish. Labrum reddish-brown. Palpi yellowish-brown. Scape of antennae yellow, apex brown on inner side; flagellum (missing after third antennal segment) brown above, yellowish-brown below. Thorax black, following parts yellow: dorsal side of pronotum, pronotal tubercles, broad line along lateral sides, posterior  $\frac{2}{5}$  of interprescutal area, axillae, scutellum except a narrow brown mark along posterior margin, metanotum, propodeum except a broad black band above (with two lateral downward projections) and a narrow band at apex, anterior plate of mesepisternum, a vague large spot on mesopleura below, behind anterior oblique suture, a small spot below fore wings and a larger one below hind wings. Petiole yellowish-red, gaster pale red. Fore and mid legs yellow, back of femora more or less brown, hind legs yellowish-red with brown tarsi. Tegulae pale yellow, veins of wings brown.

Head large. Frontal carina raised, broadened and excavate between antennae, ending below antennae in a transverse carina (Fig. 23). This transverse carina is situated on a raised area which in dorsal view is protruding like a sloping roof (Fig. 25); in lateral view this area extends far beyond the surface of the clypeus (Fig. 24). Protruding median part of anterior margin of clypeus broad, indistinctly tridentate, disk of clypeus superficially punctate. Frons and vertex shining, almost impunctate, tempora slightly dull, finely punctate. Occipital carina ending in hypostomal carina. Apex of mandibles bidentate. Third antennal segment over three times as long as broad at apex.

Pronotal corners obtuse. Scutum finely aciculate, very finely and sparsely punctate. Prescutal sutures narrow, indistinctly foveolate, reaching hind margin. Scutellum and metanotum shining, almost impunctate. Enclosed area of propodeum triangular, median longitudinal groove on back of propodeum narrow, back laterally with shallow, finely transversely striate groove. Sides of propodeum, mesopleura and mesosternum shining, almost impunctate. Anterior oblique suture narrow, foveolate, upper part striate. Petiole cylindrical, nearly twice as long as first tergite, a short groove at apex. Pygidial area elongate-triangular, apex blunt (Fig. 26). Femora rather thick, base of hind tibiae with smooth narrow groove, margined on inner side by a narrow high carina, base also with long thin spine which is twice as long as width of base. First recurrent vein ending in first

submarginal cell, second recurrent vein in third submarginal cell.

Face with silvery, mostly appressed pubescence. Pubescence of rest of body yellowish-grey. Petiole dorso-laterally, laterally and ventrally with a row of long erect hairs.

Male unknown.

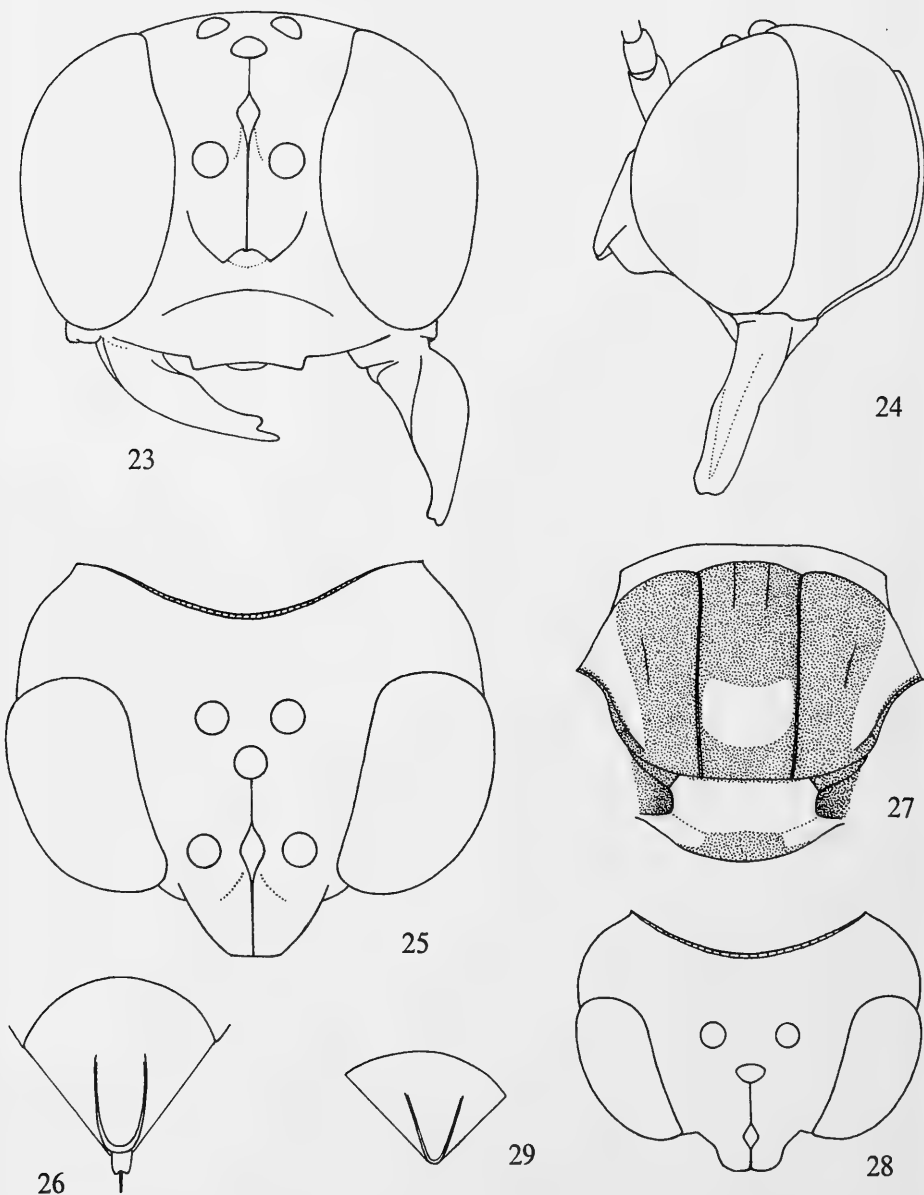


Fig. 23—26. *Psenulus tectus* sp. nov., ♀, holotype, 23—25, head in frontal, lateral and dorsal aspect; 26, pygidial area. Fig. 27—29. *Psenulus anomalus* sp. nov., ♀, holotype, 27, thorax; 28, head in dorsal aspect; 29, pygidial area

Laos: 1 ♀, holotype, Savannakhet Prov., Savannakhet, 15 April 1967, native collector (BISH).

*P. tectus* is one of the first two representatives on the Asiatic continent of the group of *Psenulus scutatus*, thus far known from the Philippine Islands, Borneo and Java. It is easily distinguished from the other species of this group by the roof-like protuberance below the antennae.

***Psenulus anomalus* sp. nov.**

Female (holotype). — Length about 6.5 mm. Head black; mandibles yellow with dark tips, palpi yellowish-brown. Dorsal half of scape brown on inner side, flagellum dorsally brown, yellowish below. Thorax (Fig. 27) black with following parts yellow: dorsal side of pronotum, pronotal tubercles, lateral margins of scutum, a large mark between prescutal sutures near hind margin, scutellum except a narrow brown mark along posterior margin, a very small spot on axillae, metanotum except narrow brown hind margin, back of propodeum except broad basal band and narrower apical margin (sides of propodeum black), upper third of anterior plate of mesepisternum. Fore and mid legs yellow, underside of fore femora brown, hind legs reddish. Petiole black, rest of gaster including ventral plate reddish. Veins of wings brown.

Head large. Frontal carina raised and excavate between antennae, ending below antennae in a projecting short transverse carina (Fig. 28). Clypeus shining, indistinctly sculptured on surface. Anterior margin of clypeus somewhat emarginate, left part deformed in the type, probably with large, blunt median tooth. Frons and vertex smooth and shining. Tempora dull. Occipital carina ending in hypostomal carina. Antennae short, clavate, segments 11-12 nearly twice as broad as long. Mandibles with blunt apex.

Pronotal corners obtuse. Scutum very finely aciculate with some fine punctures. Prescutal sutures narrow, finely foveolate, reaching hind margin. Between prescutal sutures before hind margin a number of short rugae. Parapsidal sutures long. Scutellum and metanotum smooth and shining. Enclosed area of propodeum rather narrow, the small central area connected with fore margin by a short carina (petiolate). Back and sides of propodeum smooth, median sulcus narrow, between back surface and sides a narrow area of fine irregular carination. Mesopleura smooth and shining, mesosternum more distinctly punctate. Anterior oblique suture foveolate, also widened upper part. Legs rather thick, basal  $\frac{2}{3}$  of hind tibiae with smooth groove, margined on inner side by a sharp carina, base of this groove with a narrow spine about twice as long as width of base. First recurrent vein of fore wings interstitial, second recurrent vein ending well in third submarginal cell.

Petiole almost cylindrical, nearly  $1\frac{1}{2}$  times as long as first tergite, a small triangular depression at apex. First tergite longer than broad at apex. Gaster very finely aciculate, indistinctly punctate. Pygidial area (Fig. 29) triangular.

Pubescence of face and tempora silvery, mostly appressed. Pubescence of rest of body whitish, dense on mesosternum; epicnemial areas below with a small, densely pubescent spot. Petiole with long lateral and ventral erect hairs, dorso-laterally a row of fine short hairs, intermixed with a few long hairs.

Male unknown.

Vietnam: 1 ♀, holotype, 15—35 km NW. of Phan Rang, 8—16 Nov. 1960, C.M. Yoshimoto (BISH).

Although the clypeal margin is deformed, the other characteristics, especially the shape of the pygidial area justify the naming of this form as a distinct species. *P. anomalus* is the first representative of the group of *P. scutatus* in Vietnam and the second known species of this group on the Asiatic continent.

### ***Psenulus quadridentatus* Van Lith**

Van Lith, 1962: 37—38 (Malaya); 1972: 162 (Vietnam); 1973: 133 (Nepal).

New record from Malaya: 1 ♀, Pahang, Cameron Highlands, 5000 ft, 29 April 1973, C.G. Roche (CGR).

### ***Psenulus chillcotti* Van Lith**

Van Lith, 1973: 133—136 (Nepal).

First record from Burma: 1 ♀, NE. Burma, Kambaiti, 7000 ft, 1 May 1934, R. Malaise (BM).

### ***Psenulus vaneuensis* sp. nov.**

Male (holotype). — Length 5—6 mm. Head black; labrum reddish, palpi yellowish-brown, flagellum of antennae dark brown, underside and scape reddish-brown. Thorax black, pronotal tubercles yellowish-red. Legs including trochanters and apex of coxae reddish, underside of fore and mid femora brown. Gaster including petiole red.

Clypeus convex, surface densely superficially punctate, anterior margin bidentate. Interantennal carina broadened, this part more than twice as long as wide, carina ending in a transverse carina below antennae. Frons and vertex shining, superficially finely punctate, tempora more densely punctate. Occipital carina ending in hypostomal carina. Antennae moniliform, segment 3 nearly twice as long as broad at apex, following segments gradually decreasing in length, segments 8—11 about as long as greatest width, segment 12 slightly longer than broad, segment 13 nearly twice as long as broad at base. Segments 3—12 with distinct, dark, oblong tyloidea, about twice as long as broad, small on segment 3.

Pronotal corners obtuse. Scutum shining, densely, mostly finely, punctate. Prescutal sutures foveolate, about as long as anterior  $\frac{3}{4}$  of scutum. Scutellum shining, finely punctate. Metanotum dull, densely minutely punctate. Enclosed area of propodeum rather narrow, lateral parts with oblique carinae. Back of propodeum dorsally smooth and shining, declivous part finely punctate, apex with a few rugae, dorso-laterally a broad, coarsely foveolate groove. Posterior part of sides of propodeum irregularly carinate. Mesopleura shining, finely punctate, interstices a few times size of punctures. Hypo-epimeral area minutely punctate. Mesosternum densely finely punctate. Anterior oblique suture broad, foveolate, also widened upper part. Petiole thick, about as long as first tergite, dorsally



convex, ventrally keeled, sides somewhat depressed. Gaster shining, minutely punctate.

Genitalia (Fig. 30) yellowish-brown, apex of basiparameres on inner side projecting as a low tooth, apex of parameres rounded.

Pubescence greyish-white.

Female unknown.

Laos: 1 ♂, holotype, Vientiane Prov., Ban Van Eue, 15 May 1966, native collector (BISH).

*P. vaneuensis* seems to be closely related to *P. chillcotti*, which also belongs to the group of *P. quadridentatus*. The genitalia, however, are different (cf. Van Lith, 1973).

### ***Psenulus puncticeps* (Cameron)**

Cameron, 1907: 91 (*Psen puncticeps*; India).

Rohwer, 1923: 595—596 (*Diodontus antennatus*; Singapore).

Van Lith, 1962: 44—46 (*Psenulus antennatus*; Malaya, Java, Bali); 1973: 136—137 (*Psenulus puncticeps*; Nepal).

First records from Laos: 1 ♀, Sayaboury Prov., Sayaboury, 17 Febr. 1965, native collector, 1 ♀, Vientiane Prov., Ban Van Eue, 750 m, forest streambed, 10—11 April 1965, J.L. Gressitt, Malaise trap (BISH).

In these females the pronotal tubercles are yellowish, the petiole is reddish-brown or dark brown, with reddish apex and ventral plate.

First record from Flores: 1 ♀, C. Flores, Moni, Wolowaru, 11 Nov. 1949, Bühler and Sutter (NMB).

This female is rather dark. Pronotal tubercles blackish-brown on fore part, yellowish-brown behind. First tergite almost entirely black, also petiole with ventral plate. Apical  $\frac{2}{3}$  of hind tibiae brownish-black, mid tibiae slightly brownish.

Genitalia of a male from Malang, Java: Fig. 31, 32.

### ***Psenulus puncticeps rufipes* subsp. nov.**

A male from West Sumba much resembles the males of the nominate form from Java and Bali. It differs in having the hind legs including trochanters completely reddish and there is no yellowish ring on the base of the hind tibiae. Fore and mid legs yellowish-red, femora brownish below. Ventral plate of petiole and first tergite reddish. Posterior half of pronotal tubercles brownish.

Antennal segments less rounded than in the nominate form, segments 3—10 with small but distinct tyloidea. The males from Java and Bali have indistinct tyloidea on segment 4—9, which have not been mentioned earlier.

W. Sumba: 1 ♂, holotype, Pogobina, 16 Sept. 1949, Bühler and Sutter (NMB).

### ***Psenulus exiguus* sp. nov.**

Female (holotype). — Length about 6 mm. Head and thorax black, mandibles dark brown, palpi brown. Antennae dorsally dark brown, ventrally yellowish-

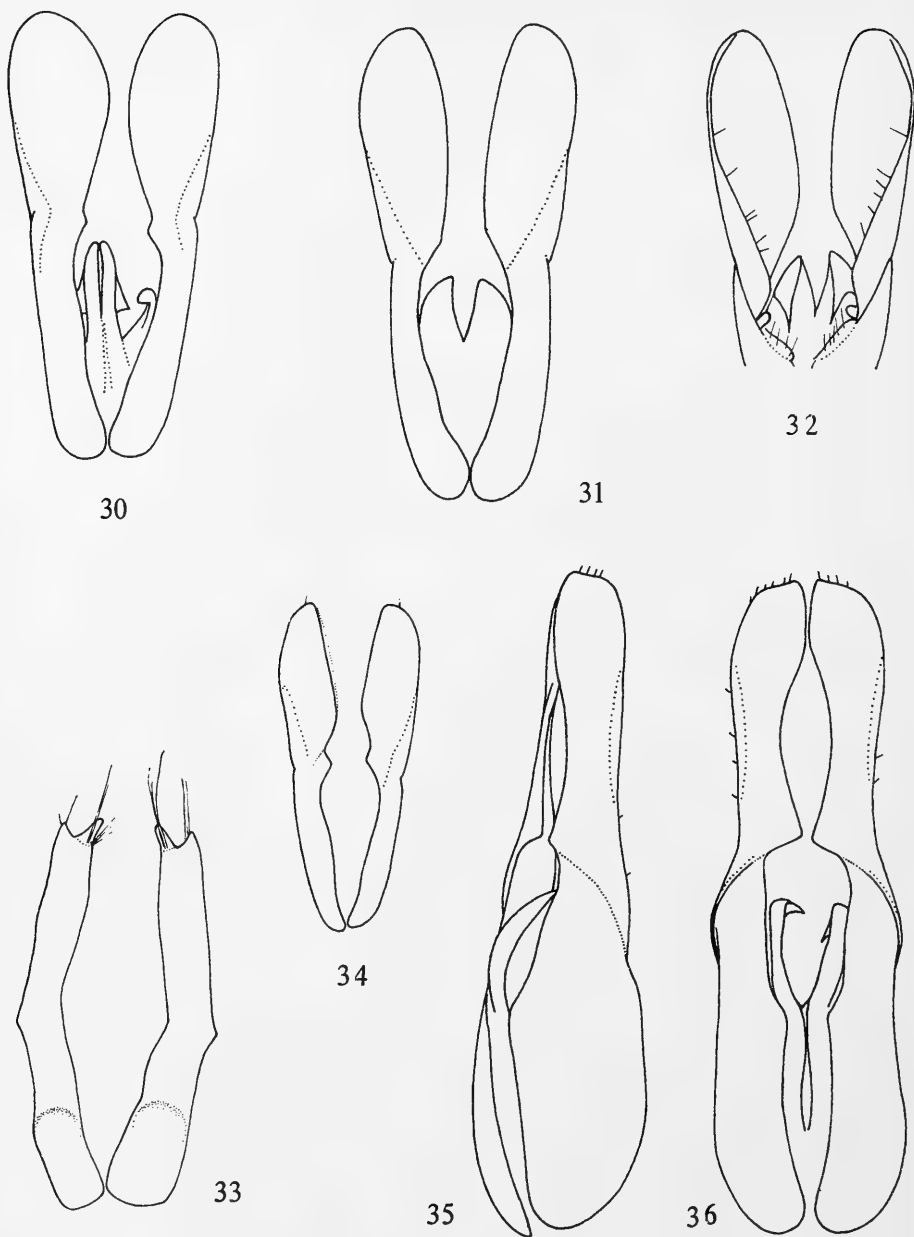


Fig. 30—36. Male genitalia of various species of *Psenulus*. 30, *P. vaneuensis* sp. nov., holotype, dorsal aspect; 31—32, *P. puncticeps* (Cameron), Java, dorsal and ventral aspect; 33, *P. crabroniformis wapiensis* subsp. nov., paratype; 34, *P. exiguus* sp. nov., paratype, Malaya; 35—36, *P. suturalis* sp. nov., holotype, lateral and dorsal aspect

brown. Pronotal tubercles brownish-yellow. Femora brown, tibiae and tarsi yellowish-brown. Petiole dark brown. Gaster dark reddish, first tergite and apical half of tergites 2—3 and base of fourth tergite blackish (irregular, discoloured?).

Raised part of interantennal carina broadened and excavate. No distinct transverse carina. Median part of clypeal margin with two small teeth. Frons and vertex shining, finely but distinctly, rather densely, punctate. Tempora finely striate. Occipital carina ending in hypostomal carina. Mandibles tridentate at apex. Antennae short, clavate, segments 6—10 shorter than broad at apex, last segment about  $1\frac{1}{2}$  times as long as broad at base.

Pronotal corners obtuse. Scutum shining with some irregular, mostly fine, punctation. Prescutal sutures indicated on posterior part of scutum by a few irregular rows of punctures. Hind margin of scutum with short rugae. Enclosed area of propodeum narrow, central area and sulcus on back of propodeum rather wide, sulcus with some transverse carinae. Back of propodeum shining, laterally an irregularly carinate edge. Mesopleura shining, almost impunctate. Anterior oblique suture narrow, foveolate, widened upper part with a few transverse carinae. Legs normal. First recurrent vein of fore wings interstitial, second recurrent vein ending in third submarginal cell. Petiole subquadrate in cross-section, about  $1\frac{1}{2}$  times as long as first tergite. First tergite about as long as broad at apex, tergites densely finely punctate. Pygidial area indistinct.

Pubescence of face, tempora and pronotum silvery, mostly appressed. Thorax whitish pubescent, mesosternum very densely so, also a small round patch on epicnemial areas below. Gaster yellowish pubescent.

Male. — Resembling female. Length 6—6.5 mm. Tergites 1, 3 and following brown. Apical outer half of hind tibiae brown. Normal transverse carina below antennae. No distinct tyloidea. Back and dorsal part of propodeum with fine oblique striation.

Genitalia (Fig. 34) yellowish-brown, parameres largely transparent. Apex of basiparameres with inconspicuous small tooth, apex of parameres rounded.

Laos: 1♀, holotype and 1♂, allotype, Sayaboury Prov., Sayaboury, 13 April 1966, native collector (BISH).

Malaya: 1♂, paratype, Selangor, Ulu Langat, 300—390 m, 13 June 1958, T.C. Maa (BISH).

The male from Malaya is slightly different in colour. Petiole and first tergite, apical  $\frac{2}{3}$  of tergite 2, apical half of tergite 3 and tergites 4—7 dark brown. Only back of propodeum with oblique striae.

*P. exiguus* belongs to the group of *P. puncticeps*. It differs from *P. puncticeps* which has been taken at the same locality in Laos, by the small size and the extension of the dark brown colour.

#### *Psenulus suturalis* sp. nov.

Male (holotype). — Length about 8.5 mm. Head black; mandibles dark reddish, palpi brown. Antennae dark brown, reddish-brown below. Thorax black, hind margin of pronotal tubercles and tegulae reddish-brown. Foreside of fore and mid femora, whole fore and mid tibiae and tarsi and greater part of hind tibiae reddish-

brown, rest of legs brown. Veins of wings dark brown. Petiole black, gaster including ventral plate of petiole reddish.

Raised part of interantennal carina narrow, ending below antennae in a long transverse carina. Clypeus densely superficially punctate, anterior margin with two small teeth. Frons, vertex and tempora smooth and shining. Occipital carina ending in hypostomal carina. Antennae long, third segment more than twice as long as broad at apex, segments 4—12 about twice as long, segment 13 more than twice as long as broad at base. No tyloidea, segments 4—10 with indistinct tubercles.

Pronotal corners about rectangular. Scutum, scutellum and metanotum shining, sparsely finely punctate. Prescutal sutures almost reaching hind margin, broad, foveolate. Enclosed area of propodeum and sulcus on back of propodeum deep. Behind enclosed area of propodeum some indistinct longitudinal striation, back and sides of propodeum very coarsely reticulato-carinate. Mesopleura and mesosternum smooth and shining, sparsely minutely punctate. Anterior oblique suture broad and coarsely foveolate, also widened upper part. Legs normal, slender. First recurrent vein of fore wings ending in first submarginal cell, distance from second submarginal cell about  $\frac{1}{3}$  of abscissa of radius in the second cell. Second recurrent vein ending in third submarginal cell. Petiole broad, widening towards apex, slightly longer than first tergite. Petiole dorsally with two parallel, broad, rounded carinae, laterally with deep groove, ventral side flattened. First tergite longer than broad at apex. Tergites shining, sparsely finely punctate.

Genitalia (Fig. 35, 36) long and narrow, reddish-brown, broadened part of parameres almost black. Parameres on inner side basally broadened into a large triangular tooth, parameres towards apex gradually broadening, apex with small tooth on inner side. Between basiparameres and parameres a high, rounded ridge on dorsal side.

Pubescence of face silvery-white, mostly appressed. Tempora with long whitish pubescence. Vertex and thorax with greyish-brown pubescence, dense on mesosternum. Gaster with yellowish-brown pubescence. Petiole dorso-laterally, laterally and ventrally with long erect hairs.

Female unknown.

Laos: 1 ♂, holotype, Vientiane Prov., Ban Van Eue, 15—31 May 1965, native collector (BISH).

*P. suturalis* is distinguished by the coarse and long prescutal sutures, the structure of the petiole and the genitalia. It does not fit well into any of the Indo-Australian species-groups described thus far.

### ***Psenulus erraticus basilanensis* (Rohwer)**

Rohwer, 1921: 318—319; 1923: 595 (*Diodontus basilanensis*; Basilan, Singapore).

Van Lith, 1962: 49—50 (*Psenulus erraticus basilanensis*); 1970: 95—96 (Tawi Tawi).

New record from Singapore: 1 ♂, University of Singapore, Campus, 8 May 1972 (US).

Pubescence of face silvery, of frons, thorax and gaster yellowish-golden (fresh

specimen), hairs long on metanotum. Petiole with lateral row of short hairs, sides with long hairs directed obliquely downwards.

This is the second known male of *P. basilanensis*. Both have been collected in Singapore.

### ***Psenulus crabroniformis crabroniformis* (Smith)**

Smith, 1858: 107 (*Mellinus crabroniformis*; Borneo).

Van Lith, 1962: 51—53 (*Psenulus crabroniformis*); 1972: 168—170 (Thailand).

Tsuneki, 1974: 637—638 (Malaya).

New record from Malaya: 1 ♀, Pahang, Genting Serpah, 2100 ft, 2 Dec. 1973, C. G. Roche (CGR).

New record from Thailand: 1 ♀, 50 km W. of Tak, 900 m, 7—8 April 1966, J. and M. Sedlacek (BISH).

First records from Laos: 6 ♀, Sayaboury Prov., Sayaboury, 12 Febr., 2 March and 13 April 1966, two in Malaise trap; 2 ♀, Vientiane Prov., Ban Van Eue, 29 March and 31 May, 1966, native collector (BISH).

The petiole is reddish, base somewhat paler. In the female from Pahang the sides of the petiole are slightly darkened apically. OOD : POD = 9 : 7 (OOD is distance between oculi and ocelli, POD is distance between posterior ocelli).

### ***Psenulus crabroniformis wapiensis* subsp. nov.**

Four males from Laos differ from the nominate form (cf. Van Lith, 1962) in the sculpture of the thorax. The punctures are strong, the interstices often smaller than the punctures; in two specimens there are short transverse rugae across the prescutal sutures. The mesopleura are distinctly punctate, interstices mostly larger than punctures. In one specimen (15 March 1967) the apical half of the petiole is dark brown.

Genitalia (Fig. 33) with slender parameres, deeply emarginate at apex and with some long hairs at apex.

Female unknown.

Laos: 2 ♂, holotype and paratype, Wapikhamthong Prov., Wapi, 30 March 1967, 2 ♂, paratypes, 15 March and 15 April 1967, same locality, native collector, light trap (BISH).

### ***Psenulus crabroniformis nathani* subsp. nov.**

Female (holotype). — Differs from the nominate form from Thailand and Malaya by the darker petiole (more than apical half black, base yellowish), the almost entirely black instead of reddish hind femora and the dorsally dark brown apical half of the hind tibiae.

Pubescence of face and tempora silvery-white, of vertex greyish-brown, of thorax greyish or whitish. OOD : POD = 9 : 7.

Male unknown.

South India: 1 ♀, holotype, Anamalai Hills, Cinchona, 3500 ft, May 1967, P.S. Nathan (MA).

***Psenulus crabroniformis sumatranus* (Ritsema)**

Ritsema, 1880: 225—226 (*Psen sumatranus*; Sumatra).

Van Lith, 1962: 53—54 (*Psenulus crabroniformis sumatranus*; Sumatra, Java).

New records from West Java: 1 ♀, Mt. Gedogan, Djampang Tengah, Oct. 1937, 1 ♀, Mt. Melang, Djampang Wetan, 3—7000 ft, Dec. 1937, 1 ♀, Mt. Malang, 3—4000 ft, K. M. Walsh (BM).

In the Javanese form OOD : POD appears to be 10.5: 7.

***Psenulus philippinensis philippinensis* (Rohwer)**

Rohwer, 1921: 317—318 (*Diodontus philippinensis*, Luzon).

Van Lith, 1962: 54—56 (*Psenulus philippinensis philippinensis*).

New record: 1 ♀, Philippine Is., Luzon, Mt. Limay, Baker (USNM).

Thus far the nominate form is restricted to Luzon, where in total nine females have been collected.

***Psenulus philippinensis dapitanensis* (Rohwer)**

Rohwer, 1923: 594—595 (*Diodontus dapitanensis*; Mindanao).

Van Lith, 1962: 56 (*Psenulus philippinensis dapitanensis*; Mindanao, Bohol).

New records from Philippine Is.: 1 ♀, Biliran, Baker (USNM); 1 ♂, Negros, Cuernos Mts, Baker (USNM).

First description of male. — Length about 8.5 mm. Resembling female. Face with golden pubescence. Pubescence of thorax golden-brown. Hind femora dorsally not brownish, as in the female from Biliran, but all legs entirely yellowish-red, also antennae except scape which is more yellowish, flagellum dorsally not brownish, as in female.

Antennal segments 3—10 about 1½ times, segments 11—12 about 1½ times as long as broad at apex, last segment twice as long as broad at base. No tyloidea. Scutum resembling that of nominate subspecies, but with tendency to transverse rugosity.

Genitalia (Fig. 37—38) slender, yellowish-brown. Parameres with small triangular flag about halfway inner side, apex with large tooth on inner corner and a few long hairs. A few bristles on underside of parameres near apex. Apex of seventh sternite with small triangular emargination. Apical margin of sixth sternite (Fig. 40) very finely serrate. Eighth sternite Fig. 39.

Notwithstanding the sculpture of the scutum I consider this male to belong to *dapitanensis*, mainly because of the blackish apical ⅔ of the petiole.

***Psenulus maculatus maculatus* Van Lith**

Van Lith, 1962: 61—62 (Malaya).

New record: 1 ♀, Singapore, Changi Beach, 7 July 1972 (US).

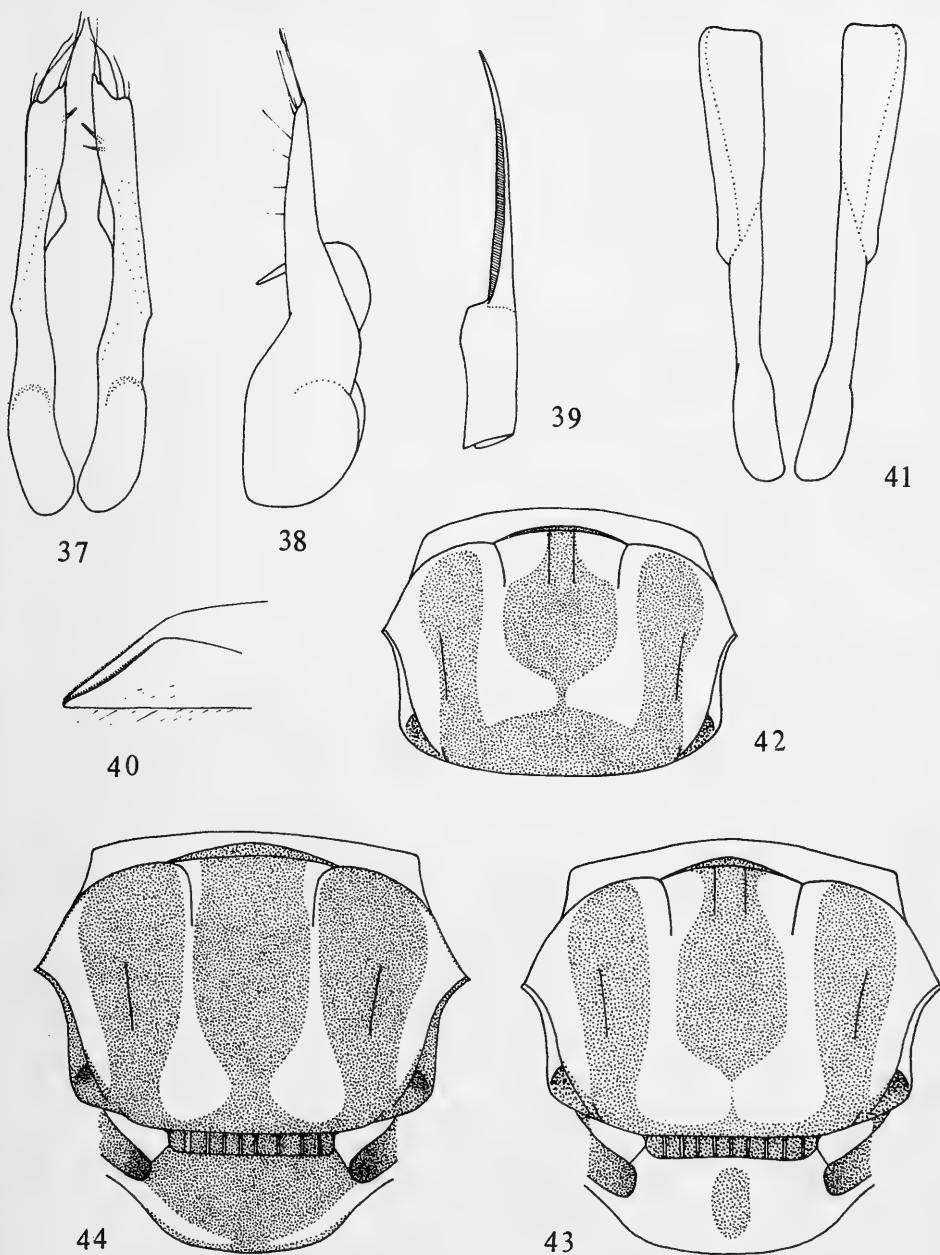


Fig. 37—40. *Psenulus philippinensis dapitanensis* (Rohwer), ♂, Negros, 37—38, genitalia, dorsal and lateral aspect; 39, 8th sternite, lateral aspect; 40, 6th sternite, lateral aspect. Fig. 41—42. *Psenulus trimaculatus* Van Lith, ♂, paratype, 41, basiparameres and parameres, dorsal aspect; 42, pronotum and scutum. Fig. 43. *Psenulus varius* Van Lith, ♀, thorax, dorsal aspect. Fig. 44. *Psenulus limbatus* sp. nov., ♀, holotype, thorax, dorsal aspect

***Psenulus trimaculatus* Van Lith**

Van Lith, 1962: 80—81 (Malaya).

New records: 3 ♂, Singapore, Bukit Timah Forest, 26 April 1973, D. H. Murphy (US); 1 ♂, Malaya, Kepong, 130—300 m, 13—21 March 1966, light trap, J. Sedlacek (BISH).

These males are darker than the holotype from Penang. The lateral marks on the scutum reach the black hind margin (Fig. 42), the median mark is connected with the hind margin by a narrow or indistinct line. Axillae black, with smaller or larger yellow spot. Third antennal segment over twice as long as broad in frontal view, segments 4—6 about twice, segments 7—10 about 1½ times, segments 11—12 about twice as long as broad at apex, last segment about 2½ times as long as broad at base. No tyloidea.

Genitalia (Fig. 41) straw-yellow, apex straight.

The marking of the scutum much resembles that of *P. peterseni* Van Lith, from the Philippine island Tawi-Tawi, of which only females are known. However, *peterseni* has the anterior plate of the mesepisternum largely yellow instead of entirely black, whilst the hypo-epimeral area is partly black, instead of entirely yellow as in the male of *P. trimaculatus*. Also the petiole of *P. peterseni* is different. Both species belong to the group of *P. sandakanensis*.

With regard to the three males from Singapore I received the following note from Dr. D. H. Murphy, Singapore: "Specimens of *Psenulus* reared from nests in vertical dead sapling in heavily shaded forest valley near small stream. Nests were in holes apparently made by larvae of *Therates dimidiatus* Dei. (Coleoptera: Cicindelidae) and several similar holes were still occupied by *Therates* larvae. Prey residues from one chamber were examined and contained recognisable fragments of Aphididae only, including siphons probably belonging to *Greenidoidea* sp. The forest belongs to "Tropical Moist Forest" (Holdridge classification). Nests were between 3 and 4 feet above ground level."

Dr. Murphy kindly also sent me one of the nests. It contains three empty cells, each about 8 mm long, diameter over 3 mm. The head end of the cells is closed by a brown lid, on the outer side with some fine white silk threads; the inner side is lined with a white layer which continues for about 1 cm on the sides. Between the first and second cell and between the second and third cell there is also a thin partition of macerated pith.

***Psenulus varius* Van Lith**

Van Lith, 1962: 69—70 (Malaya); 1972: 176—177.

New records: 5 ♀, Malaya, Penang, Tanjong Bungah, Sungei Kechil, 21—24 Jan. 1964, 1 ♀, Malaya, Penang, Penang Hills, Sungei Pinang, 16 May 1964, H. T. Pagden (BM).

There is some variation in the marking of the scutum (Fig. 43). In five of the six females the narrow line which connects the median mark with the hind margin is more or less indistinct, interrupted or even absent. The black mark of the



scutellum is either triangular or reduced to a median longitudinal mark.

The first recurrent vein of the fore wings is sometimes almost interstitial.

***Psenulus limbatus* sp. nov.**

Female (holotype). — Length about 8 mm. Head black; apical margin of clypeus and labrum reddish, mandibles except apices yellow, palpi yellowish. Scape of antennae and underside of segments 2 and 3 yellow, rest of underside of flagellum yellowish-red. Thorax black except the following parts. Dorsal side of pronotum and pronotal tubercles yellow. Scutum yellow with three broad black bands reaching fore and hind margin (Fig. 44). Axillae yellow, scutellum with yellow hind margin, interrupted in the middle. Metanotum, back of propodeum, upper  $\frac{1}{3}$  of anterior plate of mesepisternum and a vague spot on mesopleura near foreside yellow. Fore and mid legs and hind coxae yellow, hind femora and tibiae yellowish-red with brownish outer side, hind tarsi brown. Gaster including petiole yellowish-red. Veins of wings brown.

Anterior margin of clypeus hardly emarginate, with two small teeth; distance between these teeth about  $\frac{1}{5}$  of total distance there between the eyes. Interantennal carina dorsally sharp, ending below antennae in a transverse carina. Frons, vertex and tempora shining, almost impunctate. Postocellar area not raised. Occipital carina ending in hypostomal carina. Third antennal segment about  $2\frac{1}{2}$  times, segments 4—6 about twice, segments 7—11 about  $1\frac{1}{2}$  times as long as broad at apex, segment 12 about  $2\frac{1}{2}$  times as long as broad at base.

Scutum, scutellum and metanotum shining, distinctly finely punctate. Enclosed area of propodeum triangular, dorsal part of pronotum shining, back and posterior half of sides of propodeum densely finely reticulate, median groove narrow. Mesopleura, hypo-epimeral area, anterior plate of mesepisternum and mesosternum shining, indistinctly punctate. Legs slender. First recurrent vein of fore wings interstitial. Petiole cylindrical, little longer than first tergite. Pygidial area long and narrow, apically with almost parallel carinae.

Pubescence of face silvery, mostly appressed, of rest of body whitish.

Laos: 1 ♀, holotype, Vientiane Prov., Gi Sion Vill., de Tha Ngone, 21—28 Febr. 1966, native collector (BISH).

Because of the transverse carina below the antennae *P. limbatus* has been placed in the group of *P. esuchus*. It resembles somewhat the male of *P. fyanensis* from Vietnam and Laos. However, fore and mid femora and tibiae are entirely yellow, the anterior plate of the mesepisternum is more distinctly yellow, and the propodeum is less dark. Certainty regarding the status of these two forms can be obtained only when the opposite sexes are found.

***Psenulus impressus* sp. nov.**

Male. — Length about 6 mm. Head black; mandibles yellow except dark tips, palpi pale yellow. Scape of antennae yellow, flagellum yellowish-brown below, dark brown above. Thorax yellow with narrow black mark along hind margin of scutum, this mark anteriorly roundly extended. Black parts: posterior corners of

scutum, anterior and lateral depressed parts of scutellum, enclosed area of propodeum and median longitudinal sulcus on back of propodeum, a small mark below fore wings, interepicnemial area and a narrow median line on mesosternum. Fore and mid legs including coxae and hind coxae yellow, rest of hind legs reddish-yellow, gaster including petiole reddish, apical spine brown. Veins of wings dark brown.

Clypeus superficially punctate, margin depressed, slightly triangularly emarginate, two short triangular teeth. Raised part of interantennal carina narrow, ending below antennae in a transverse carina. Frons and vertex shining, with very fine and dense, hairbearing punctation. Interocellar area much raised, bare and shining. Upper part of back of head sloping obliquely downward from hind margin of posterior ocelli to occipital carina. Occipital carina ending in hypostomal carina. Antennae long and slender, segments 3—12 about twice as long as broad at apex, last segment about  $2\frac{1}{4}$  times as long as broad at base. No tyloidea.

Pronotal corners obtuse. Scutum with large superficial punctures, interstices mostly smaller than punctures. Prescutal sutures distinct on anterior half of scutum. Area around median scutal lines and parapsidal sutures impressed, which is best seen in anterior aspect. Scutellum and metanotum sparsely superficially punctate. Propodeal enclosed area with large central hexagonal area, lateral parts with few oblique carinae. Back of propodeum coarsely reticulato-carinate, upper part finely obliquely striate. Anterior oblique suture narrow, foveolate, widened upper part smooth. Legs slender. First recurrent vein of fore wings ending in second submarginal cell, nearly interstitial, second recurrent vein ending in third submarginal cell. Petiole cylindrical, longer than first tergite, gaster slender.

Pubescence on face, tempora and frons silvery, mostly appressed on clypeus, on ventral side of thorax dense, whitish, on rest of head and body yellowish-grey or yellowish-golden.

Genitalia (Fig. 46) small, pale brownish-yellow. Parameres dark brown, largely transparent, apex blunt.

Female unknown.

Philippine Is.: 1 ♂, holotype, Mt. Montalban, Rizal, Wa-wa Dam, 150—200 m, 2 March 1965, L. M. Torre Villas, 2 ♂, paratypes, same locality, 3 and 14 March 1965, H. M. and L. M. Torre Villas (BISH).

### ***Psenulus interstitialis interstitialis* Cameron**

Cameron, 1906: 222—223 (*Psenulus? interstitialis*; New Guinea).

Van Lith, 1962: 84—86 (*Psenulus interstitialis interstitialis*); 1972: 182—184 (New Guinea, Papua).

As stated earlier (Van Lith, 1972), this is a variable form which is also shown by the undermentioned specimens.

Lower half of anterior part of pronotum usually black, in some specimens entirely yellow. Scutum entirely yellow or with central square black mark. Antennal flagellum sometimes completely yellowish-red, usually dorsally more or less darkened. There does not seem to be any correlation between the varieties and their collecting localities; males from Mamai Plantation have either an

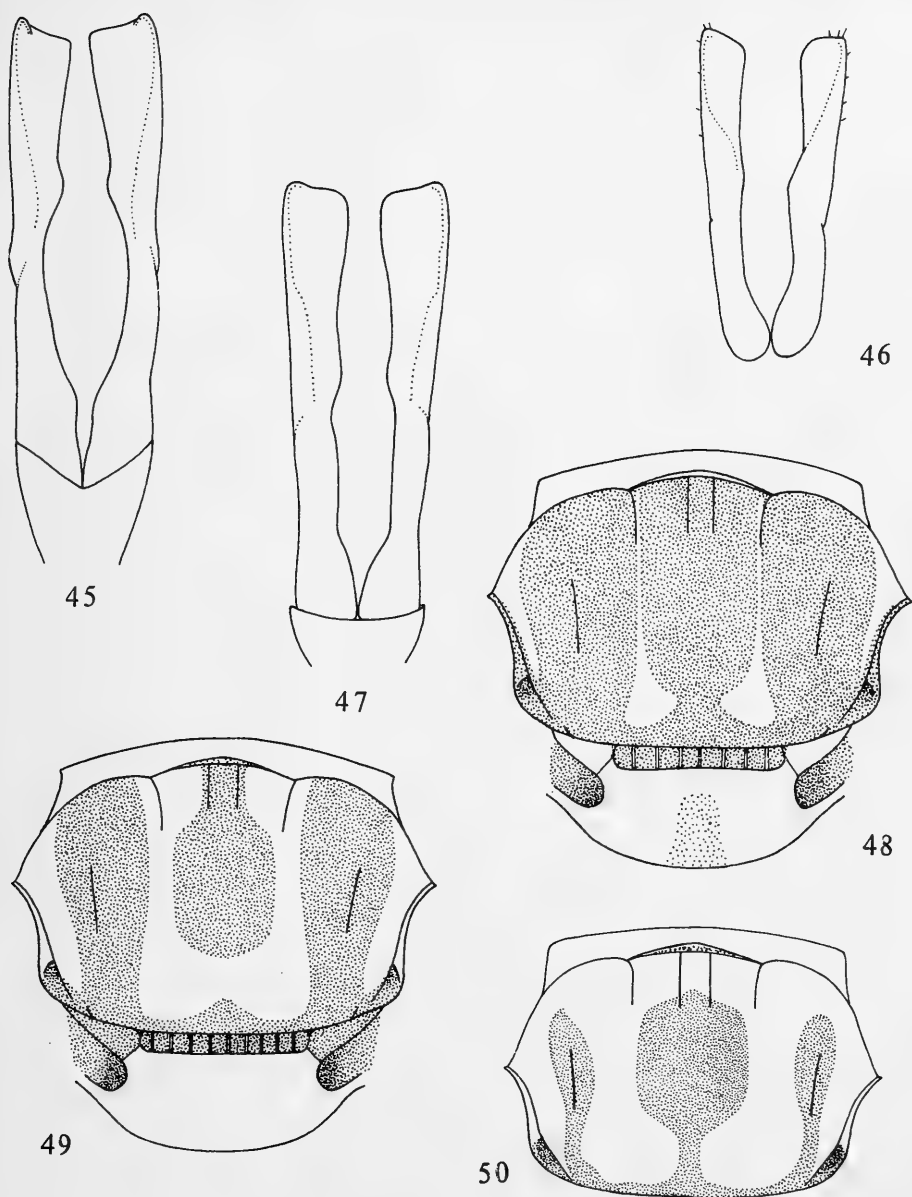


Fig. 45—47. Male genitalia of various new species of *Psenulus*. 45, *P. ventionensis*, holotype; 46, *P. impressus*, paratype; 47, *P. fyanensis*, holotype. Fig. 48—50. Thorax in dorsal aspect of various new species of *Psenulus*. 48, *P. fyanensis*, ♂, holotype; 49, *P. nigrolateralis*, ♀, holotype; 50, *P. pictus*, ♂, paratype

entirely yellow scutum and pronotum or scutum with black mark and lower part of pronotum black.

New records from NE. New Guinea: 1 ♀, May River, 6 June 1963, R. Straatman, light trap; 1 ♀, Wau, Bulolo River, 850—900 m, 24 Aug. 1965, J.

Sedlacek, Malaise trap; 1 ♂, Bulolo, 750 m, 5 Oct. 1965, J. Sedlacek, Malaise trap; 1 ♂, Wau, 1400 m, 27 Sept. 1969, A. B. Mirza; 1 ♂, Sepik, Angoram, 20—30 m, 14—16 Aug. 1969, J. L. Gressitt; 1 ♀, Baiyer River, 1000 m, 1—4 Sept. 1969, Y. Hirashima (BISH).

SE. New Guinea: 1 ♀ and 3 ♂, Mamai Pltn, E. of Port Glasgow, 150 m, 16 Febr. 1965; 2 ♂, same locality, 27 Febr. 1965, 1 ♂, Milne Bay, abt. 10 m, March 1965, all R. Straatman, light trap; 1 ♂, Cape Killerton, 0—5 m, 6—13 May 1965, W. A. Steffan, Malaise trap; 1 ♀, Central Dist., 3.2 km S. Vanapa River, Brown Road, 22—24 May 1965, W. A. Steffan and Y. M. Huang (BISH).

Papua: 1 ♀, Laloki Exp. Station, 10—17 June 1971, J. Stibick; 1 ♂, N. Dist., Onombususu, 26—28 Aug. 1971, J. Stibick (HT). Both specimens from Papua have an entirely yellow scutum.

Two females from NE. New Guinea, Green River - Sepik River junction, 200 m, 22 June and 27—28 June 1965, collected by R. Straatman with light trap (BISH) have yellowish-red thorax, antennae and fore and mid legs and resemble the subspecies *salomonensis* (Van Lith, 1972). As there are a few minor differences their identification is still uncertain.

### ***Psenulus pictus* sp. nov.**

Five males, closely related to *P. interstitialis*, are much more richly marked with black, especially on scutum and mesosternum.

Black parts: a large longitudinal mark on scutum (Fig. 50) connected by a narrow line with triangle against posterior margin and two narrow lateral marks, covering the parapsidal sutures and connected with hind margin of scutum, enclosed area of propodeum with adjacent lateral spots on declivous part, median longitudinal groove and apical margin of declivous part, depressed lateral parts of scutellum and metanotum, epicnemium except lateral margin, mesosternum, marking roundly dilated on to mesopleura and connected with broad hind margin of mesopleura, which also covers hind margin of hypo-epimeral area.

Fore and mid legs including coxae and trochanters and hind coxae yellow, tarsi of fore and mid legs and hind legs except coxae orange-red. Gaster and petiole orange-red. Antennal segments 3—13 dorsally black, underside orange-red, often brownish on apical half. Veins of wings yellowish-brown.

Black marks on mesopleura in some specimens somewhat reduced. Lateral marks on scutum, in one case also median mark, not connected with hind margin. Length about 8.5 mm.

Various species belonging to the group of *P. interstitialis* are subject to much variation, especially *P. interstitialis*, but no transitional forms have been found at Wau, where also *P. interstitialis* occurs. After some hesitation I decided to consider the described males as a distinct species. The study of more material, especially of the female, should confirm this opinion.

NE. New Guinea: 4 ♂, holotype and paratypes, Wau, McAdam Park, 1500 m, 17 Sept. 1972, flying at *Hibiscus*, Mrs. E. van der Vecht (ML); 1 ♂, Wau, 1250 m, 4 May 1965, J. and M. Sedlacek (BISH).

***Psenulus araucarius* Van Lith**

Van Lith, 1972: 187 (Central New Guinea).

This close relative of *Psenulus interstitialis* has now also been collected in NE. New Guinea: 1 ♀, Mt. Missim, 980 m, 20 July 1969, J. L. Gressitt and Y. Hirashima (BISH).

The third antennal segment is over three times as long as broad at apex, the pygidial area is broader than in *P. interstitialis* and the base of the hind tibiae is smooth and flattened. This is the second known female, the male has not yet been found.

***Psenulus ornatus sumbaensis* subsp. nov.**

Female (holotype). — Length about 9 mm. Head black, labium reddish, mandibles yellow with dark tips, palpi yellowish. Scape of antennae yellow, flagellum reddish below, dark brown above. Thorax black with following yellow parts: dorsum of pronotum, pronotal tubercles, two partly indistinct lines on scutum, slightly broadened posteriorly and not reaching hind margin, (an indistinct brownish mark along lateral margins), two elongate marks along hind margin of scutellum, metanotum except small triangular mark on hind margin, two large marks on back of propodeum, each consisting of a pair of marks broadly connected below. Tegulae reddish. Fore and mid legs including coxae and trochanters, and hind coxae, yellow; fore and mid tarsi and entire hind legs reddish. Veins of wings brown. Gaster including petiole orange-reddish.

Raised part of frontal carina between antennae not broadened, no transverse carina below antennae. Clypeus very finely punctate, lower part more shining, margin depressed, protruding median part with two small teeth, distance between these teeth about  $\frac{1}{6}$  of total distance there between the eyes. Frons and vertex shining. Apex of mandibles bidentate, a distinct reddish-brown inner tooth. Labium slightly emarginate. Antennae slightly clavate, third segment in frontal view about three times, segments 4—6 over  $1\frac{1}{2}$  times, segments 7—8 about  $1\frac{1}{2}$  times as long as broad at apex, segments 9—11 about as long as broad, last segment about  $1\frac{3}{4}$  times as long as broad at base. Occipital carina ends normally in hypostomal carina.

Pronotal corners obtuse. Scutum, scutellum and metanotum shining, almost impunctate. Prescutal sutures short and fine. Enclosed area of propodeum triangular, ill-defined posteriorly, lateral parts with oblique striae. Propodeal longitudinal groove narrow. Upper half of declivous part of propodeum smooth and shining, lower half finely, mostly transversely, reticulato-carinate, sides more coarsely so. Metapleura impunctate, mesopleura including hypo-epimeral area and mesosternum shining, very finely sparsely punctate. Anterior oblique suture foveolate, widened upper part smooth. Apex of mid tibiae anteriorly with longitudinal ridge, posteriorly with three or four short reddish thorns. Base of hind tibiae with short longitudinal area consisting of fine red thorns. Apex laterally with three short red thorns. Inner tibial spur of hind legs bent downwards, about 30 degrees. First recurrent vein of fore wings interstitial, second recurrent vein

ending in third submarginal cell. Petiole about seven times as long as wide in the middle, in dorsal aspect, one and a half times as long as first tergite, cylindrical, dorsally somewhat flattened, a triangular pit at apex, sides with a narrow strip of fine punctures. Gaster shining with fine hair-bearing punctures. Pygidial area narrow, shining, with distinct lateral carinae.

Pubescence of head silvery, on clypeus somewhat appressed but leaving sculpture visible. Pubescence of thorax greyish, on mesosternum whitish and denser, lower part of epicnemial areas with a large round patch of appressed whitish pubescence. Pubescence of gaster yellowish-grey. Petiole with long, erect, yellowish-golden lateral hairs. Apical margins of gastral sternites 4—5 with dense short pubescence.

Male unknown.

West Sumba: 1 ♀, holotype, Rua, 1 Sept. 1949, Bühler and Sutter (NMB).

This female is undoubtedly closely related to *P. ornatus* Ritsema from East Java of which only a single male is known. However, the petiole of *sumbaensis* has no darkened apex and the legs are more reddish. *P. ornatus baliensis* (Van Lith, 1962) is very similar and has also an entirely reddish petiole but the black marking on dorsal and ventral side of its thorax is much less extensive.

### ***Psenulus ornatus baliensis* Van Lith**

Van Lith, 1962: 88—89 (*Psenulus interstitialis baliensis*; Bali).

Tsuneki (1971: 3—5) places *P. kankauensis* Strand, 1915, *P. tristis* Van Lith, 1962, *P. elegans* Van Lith, 1962 and *P. pempuchiensis* Tsuneki, 1971 as subspecies of *P. ornatus* Van Lith, 1962.

He was certainly right, the more so as there is also a difference in the colour of the veins of the fore wings. In *P. interstitialis* and its subspecies and closely related species, all restricted to the Papuan area, the veins are yellowish or pale yellowish-brown. In the other species of the group of *P. interstitialis*, including *P. luzonensis* and *P. ornatus*, the wing veins are brown.

Also *P. baliensis* has dark wing-veins and is now reclassified as a subspecies of *P. ornatus*.

### ***Psenulus fyanensis* sp. nov.**

Male (holotype). — Length about 7.5 mm. Head black; mandibles except dark tips and palpi yellow. Scape of antennae yellow, basal half of underside of flagellum yellowish, rest of antennae brown. Thorax black with following parts yellow: dorsal side of pronotum, pronotal tubercles, long narrow mark along tegulae and two median lines which are broadened near hind margin (Fig. 48), axillae, scutellum except median longitudinal brown mark, metanotum, four large marks on back of propodeum. Fore and mid legs yellow, trochanters and femora somewhat brown below, hind legs reddish-brown. Gaster including petiole reddish. Veins of wings dark brown.

Median part of anterior margin of clypeus straight, lateral teeth indistinct, separated by less than  $\frac{1}{4}$  of total distance between the eyes. Raised part of interantennal carina narrow, ending below antennae in a transverse carina. Frons

and vertex indistinctly punctate, postocellar area not raised. Occipital carina ending in hypostomal carina. Antennae long, segment 3 about  $2\frac{1}{2}$  times, segments 4—12 about twice as long as broad at apex, segment 13 about  $2\frac{1}{2}$  times as long as broad at base. No tyloidea.

Pronotal corners rounded. Scutum and scutellum shining, sparsely finely punctate. Metanotum densely superficially punctate. Behind enclosed area of propodeum a narrow shining area, back and posterior half of sides of propodeum coarsely reticulate. Hypo-epimeral area, anterior plate of mesepisternum and metapleura smooth and shining, mesopleura with distinct but superficial and rather widespread punctures, punctation on mesosternum denser. Anterior oblique suture foveolate, widened upper part with transverse carinae. Legs slender. First recurrent vein of fore wings ending in second submarginal cell, near radial sector. Petiole cylindrical, about  $1\frac{1}{2}$  times as long as first tergite which is about  $1\frac{1}{2}$  times as long as broad at apex. Gaster indistinctly punctate.

Genitalia (Fig. 47) yellowish-red, slender, inner part of parameres somewhat transparent, apex straight with slightly projecting outer tip.

Pubescence of face silvery, mostly appressed, of rest of body whitish.

Female unknown.

Vietnam: 1 ♂, holotype, Fyan, 900—1000 m, 11 July—9 Aug. 1961, N.R. Spencer (BISH).

Laos: 1 ♂, paratype, Vientiane Prov., Ban Van Eue, 31 May 1966, native collector, Malaise trap (BISH).

The male from Laos has a much darker scutellum and the first recurrent vein of the fore wings is interstitial.

The shape of the parameres points to a close relationship with *P. interstitialis* and *P. luzonensis*.

### ***Psenulus nigrolateralis* sp. nov.**

Female. — Length about 8 mm. Head black; anterior margin of clypeus reddish, mandibles except dark tips yellow, palpi yellowish-brown, labrum reddish. Scape of antennae yellow, underside of flagellum yellowish-brown, upper side dark brown. Pronotum dorsally yellow. Scutum (Fig. 49) yellow with three black lines, median line anteriorly narrowed, posteriorly not distinctly connected with hind margin. Axillae black. Scutellum and metanotum yellow. Enclosed area of propodeum black, also adjacent black spot laterally. Back of propodeum yellow, longitudinal groove and two spots at apex of propodeum black. Sides of thorax including anterior margin of sides of propodeum, and underside of thorax black. Fore and mid legs including coxae and hind coxae yellow; hind legs including trochanters yellowish-red. Gaster including petiole reddish. Veins of wings dark brown.

Median part of clypeal margin protruding, indistinctly bidentate, teeth separated by about  $\frac{1}{3}$  of total distance between the eyes. Interantennal carina narrow, no transverse carina below antennae. Occipital carina ending in hypostomal carina. Frons and vertex shining, minutely punctate, postocellar area not raised. Third antennal segment about  $2\frac{1}{2}$  times, segment 4 about twice as long as broad at

apex, following segments gradually decreasing in length, segment 11 about  $1\frac{1}{4}$  times as long as broad at apex, last segment about twice as long as broad at base.

Pronotal corners rounded. Scutum rather densely finely punctate, intermixed with larger punctures. Scutellum and metanotum sparsely finely punctate. Back of propodeum almost smooth, dorso-laterally some fine reticulation. Mesopleura and mesosternum shining, sparsely finely punctate. Anterior oblique suture foveolate, widened upper part smooth. Petiole cylindrical, about  $1\frac{1}{2}$  times as long as first tergite. First tergite little longer than broad at apex. Gaster minutely punctate, pygidial area narrow, carinae on apical half almost parallel. Legs slender. First recurrent vein of fore wings interstitial.

Pubescence of face silvery, mostly appressed. Pubescence of rest of body whitish. Epicnemial areas below with round, densely, yellowish-white pubescent patch. Sternites 4—5 apically with dense short whitish pubescence. Petiole dorso-laterally and ventro-laterally with long erect whitish hairs.

Male unknown.

Laos: 1 ♀, holotype, Vientiane Prov., Ban Van Eue, 15 Jan. 1966; 1 ♀, paratype, Sayaboury Prov., Sayaboury, 15 Jan. 1966, native collectors (BISH).

This form certainly belongs to the group of *Psenulus interstitialis* and may be a dark subspecies of *P. luzonensis* (Rohwer).

#### ***Psenulus vientianensis* sp. nov.**

Male. — Length about 8 mm. Head black; mandibles except dark tips yellow, palpi pale yellowish-brown. Labrum reddish-yellow. Scape of antennae yellow, underside of antennae yellowish-brown, upper side dark brown. Thorax black with following parts yellow: dorsal side of pronotum, pronotal tubercles, axillae, metanotum and four elongate marks on propodeum. Scutum near pronotal tubercles with small yellowish-red mark and near hind margin with two very small yellow marks. Scutellum brown and black, outer lateral margins yellow. In upper corner of anterior plate of mesepisternum a vague yellowish spot. Fore and mid legs yellow, underside of femora largely brown. Hind trochanters, femora and tarsi brown, hind tibiae more reddish. Gaster including petiole reddish. Veins of wings dark brown.

Median part of anterior margin of clypeus indistinctly bidentate, teeth separated by about  $\frac{1}{4}$  of total distance between the eyes. Raised part of interantennal carina narrow, ending below antennae in a transverse carina. Frons and vertex hardly punctate, postocellar area not raised. Occipital carina normally ending in hypostomal carina. Antennae slender, segment 3 over twice, segments 4—12 about twice as long as broad at apex, last segment over  $2\frac{1}{2}$  times as long as broad at base. No tyloidea.

Pronotal corners rounded. Scutum and scutellum shining, finely sparsely punctate. Metanotum densely, superficially, punctate. Behind enclosed area of propodeum a smooth margin which is broader laterally, this smooth area defined postero-laterally by foveolae and a high carina. Back of propodeum coarsely reticulate, also greater part of sides of propodeum. Anterior plate of mesepisternum, mesopleura, hypo-epimeral area, metapleura and mesosternum smooth and



shining, hardly punctate. Anterior oblique suture foveolate, widened upper part almost smooth. Petiole cylindrical, about  $1\frac{1}{4}$  times as long as first tergite, apex dorsally with small triangular depression. First gastral tergite about  $1\frac{1}{3}$  times as long as broad at apex. Gaster minutely punctate. Legs slender. First recurrent vein of fore wings ending in first submarginal cell or interstitial.

Genitalia (Fig. 45) long and slender, yellowish-brown, inner part of parameres somewhat transparent, apex straight with outer corner distinctly projecting backward.

Pubescence of face silvery, mostly appressed, of rest of body whitish.

Female unknown.

Laos: 1 ♂, holotype, Vientiane Prov., Ban Van Eue, 15—31 May 1965; 1 ♂, paratype, same locality, 30 Nov. 1965, native collectors (BISH).

This species undoubtedly belongs to the group of *Psenulus interstitialis*. The genitalia differ little from those of *P. fyanensis*, but the colour is darker. Like some of the related forms described here as species, it may be a subspecies, perhaps of *P. ornatus*. The material is too scanty and the study of the genitalia still too insufficient to allow more definite conclusions.

### ***Psenulus continentis* Van Lith**

Van Lith, 1962: 97—98 (Malaya).

New record: 1 ♀, Singapore, Campus of University, 5 May 1972 (US).

This female agrees with the description of the holotype which was captured in Penang, in a car. The axillae are completely yellow. Anterior oblique suture black, foveolate, widened upper part almost without sculpture.

### ***Psenulus pulcherrimus pulcherrimus* (Bingham)**

Bingham, 1896: 443 (*Psen pulcherrimus*; Tenasserim).

Van Lith, 1962: 101 (*Psenulus pulcherrimus*); 1969: 200 (Vietnam); 1973: 140—141 (subspecies?; Nepal).

As in the case of a series of specimens from Nepal the variability of *P. pulcherrimus* is again shown by 26 specimens from Laos and one male from Thailand. Most often the scutum has a large postero-median yellow mark and two narrow marks along the sides. In one third part of the specimens from Laos the lateral marks are reduced or absent and in two of the females the scutum is entirely black. On the contrary in three males from Laos and in the male from Thailand the scutum is not only yellow marked postero-medially and laterally, but also anteriorly. The anterior marks range from two small separate triangular spots (Fig. 51) to a more or less broad band (Fig. 52), in one case distinctly connected with the lateral marks (Fig. 53). Extensive yellow marking of the scutum does not run parallel with the colour of the scutellum as the two females with entirely black scutum have the scutellum completely or nearly completely yellow. On the contrary, in four males with much yellow marking of the scutum the anterior half or fourth of the scutellum is black. Hind femora, first tergite and apex of petiole

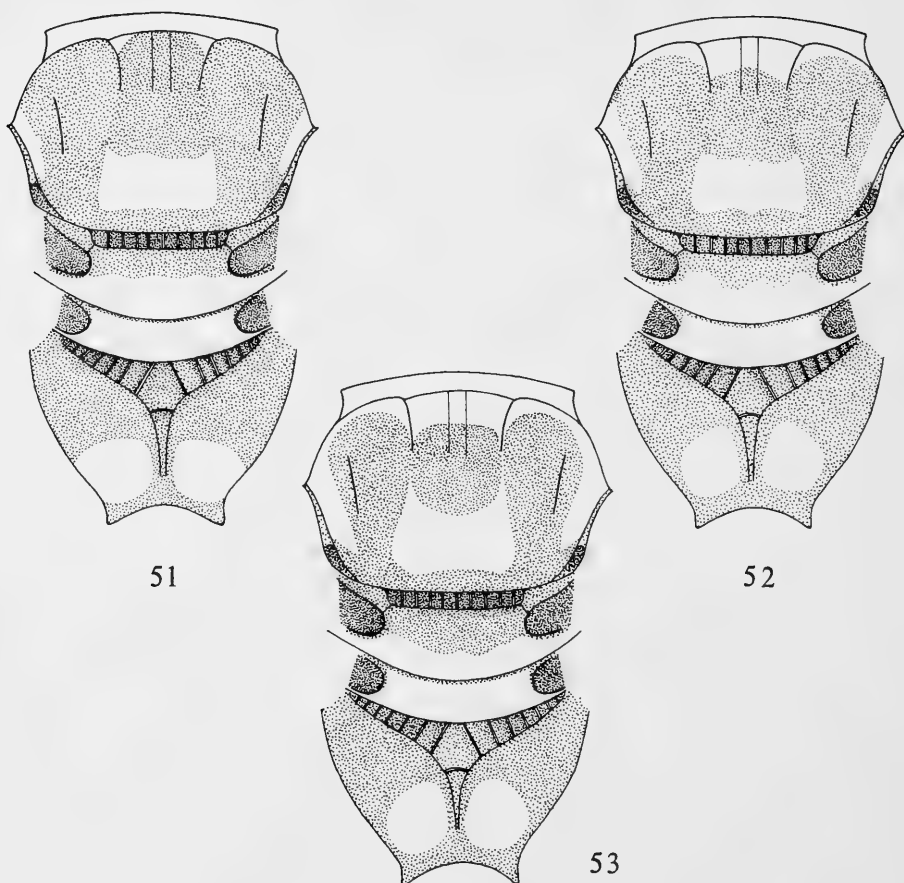


Fig. 51—53. Dorsal and posterior side of thorax of *Psenulus pulcherrimus pulcherrimus* (Bingham), ♂, 51—52, Laos; 53, Thailand

are not darkened. It seems that scutum and propodeum are richer coloured in the males, in the females the scutellum is more yellow.

Darkening of fore and mid femora occurs in the Laos material only in a few females, that of the first tergite in one female and six males. In half of the females and males the apex of the petiole and the hind femora are darkened. Both colour forms occur in the same province, even a female and a male taken on the same date in the same locality of the province of Wapikhamthong are different. Six of the seven specimens from Sayaboury have a darkened apex of petiole and hind femora whilst all of the ten specimens from Ban Van Eue in Vientiane Province have entirely reddish petiole and hind femora. In the material from Nepal the hind femora are always much darker brown, almost black and the first tergite is darkened.

In the male from Singapore recorded below the petiole is dark brown at the apex and the ventral plate is dark brown except a reddish mark near the posterior margin. The base of the first tergite is brownish-black, the hind femora except

apex are dark brown, also the apical half of the hind tibiae. Yellow marks on propodeum large. Scutellum with narrow black anterior margin.

In the female from Malaya the apex of the petiole, the base of tergite 1 and  $\frac{2}{3}$  of the hind tibiae are brown.

First records from Laos: Vientiane Prov., Gi Sion Vill., de Tha Ngone, 1 ♀, 9—16 Jan. 1966, 1 ♂, 7—21 Febr. 1965; Ban Van Eue, 4 ♀, 15—31 May 1965, 15 Febr. 1966, Malaise trap, 29 March and 30 June 1966, 6 ♂, 29 April 1966, light trap, 15 May, 15—31 May and 31 May 1966, Malaise trap, 15 Dec. 1966; Sayaboury Prov., Sayaboury, 3 ♀, 12 Febr. and 13 April 1966, 4 ♂, 15 Jan. and 2 March 1966, 2 ♂, 30 Sept. 1966, light trap; Wapikhamthong Prov., Wapi, 3 ♀, 15 March, 30 March and 31 May 1967, 3 ♂, 30 March, 15 April and 31 May 1967, light trap; Sedone Prov., Pakse, 1 ♀, 31 May 1967; Savannakhet Prov., Savannakhet, 1 ♂, 15 April 1967, all by native collector (BISH).

First record from Thailand: 1 ♂, Trang Prov., Khaophappa Khaochang, 200—400 m, 3 Jan. 1964, G. A. Samuelson (BISH).

First record from Malaya: 1 ♀, Kedah, Sungei Toh Pawang Estate, 10 Aug. 1966, H. T. Pagden (BM).

First record from Singapore: 1 ♂, Postal District 22, 26 Sept. 1970, C.G. Roche (CGR).

### ***Psenulus melanonotus* Van Lith**

Van Lith, 1969: 203 (West Sumbawa).

First record from Flores: 1 ♂, C. Flores, Moni, Wolowaru, 11 Nov. 1949, Bühler and Sutter (NMB).

This male is darker than the two males from Sumbawa. Scape of antennae pale brown instead of yellow, pronotum dorsally brown, no large yellowish-white spots, hind margin of scutellum brownish with small yellow spot, metanotum pale yellow with brown fore margin and vague median brown spot instead of being completely ivory-coloured, propodeum with two vaguely defined circular yellow spots. Only hind margin of pronotal tubercles yellowish-brown. Fore legs yellow, femora brown below; mid legs yellow, trochanters brown below, femora except apical foreside brown; hind legs brown, only dorso-basal  $\frac{2}{3}$  instead of  $\frac{1}{3}$  of hind tibiae pale yellow.

Propodeum behind enclosed area very finely striate instead of smooth.

The differences between this male and the two from Sumbawa do not seem to be of great importance.

### ***Psenulus leucognathus* sp. nov.**

Male. — Length about 6 mm. Head black; scape and mandibles ivory-white, apex of mandibles, also labrum, reddish, palpi and underside of flagellum pale yellowish. Thorax black, with following ivory-white parts: pronotum except central and lateral parts, pronotal tubercles, two lateral marks on metanotum and two small marks on back of propodeum. Tegulae reddish transparent. Trochanters, dorsal side of fore and mid femora, fore and mid tibiae except a brown mark

on back, tarsi of fore and mid legs and basal  $\frac{2}{3}$  of hind tibiae ivory-white, rest of hind legs dark brown. Petiole dark brown, hind margin of ventral plate and gaster red. Veins of wings black.

Raised part of interantennal carina narrow, ending below antennae in a transverse carina. Anterior margin of clypeus bidentate, distance between apices of teeth about  $\frac{1}{3}$  of total width of margin. Frons and vertex shining. Postocellar area narrow. Occipital carina ending in hypostomal carina. Base of antennae somewhat flattened, segments rounded below, segment 3 about twice, segments 4—9 over  $1\frac{1}{2}$  times and segments 10—12 about  $1\frac{1}{2}$  times as long as broad at apex, last segment about twice as long as broad at base. No tyloidea.

Pronotal angles obtuse. Punctuation of scutum distinct, irregular, interstices centrally a few times as large as punctures, laterally punctures finer. Scutellum and metanotum sparsely punctate. Enclosed area of propodeum triangular, with oblique carinae, back and sides of propodeum coarsely reticulate, behind enclosed area a narrow smooth area. Mesopleura and mesosternum finely sparsely punctate, hypo-epimeral area smooth. Anterior oblique suture foveolate, widened upper part with a few transverse carinae. Legs normal. Petiole about as long as first tergite, cylindrical, dorsally somewhat flattened. Gaster slender, first tergite longer than broad at apex.

Face and tempora densely, mostly appressed, silvery pubescent, rest of body whitish pubescent.

Female unknown.

South India: 1 ♂, holotype, Kerala State, Walayar Forests, 200 ft, Sept. 1959, P.S. Nathan (UI, deposited on permanent loan in USNM).

*P. leucognathus* belongs to the *Psenulus pulcherrimus*-group. It is very close to *P. melanotus* from Sumbawa, from which it differs in the red gaster and the lesser extent of the whitish marking. Both species are easily distinguished from other species of the group by the ivory-white mandibles and whitish marks on pronotum, metanotum and propodeum.

### ***Psenulus extremus* Van Lith**

Van Lith, 1966: 45—46 (*Psenulus carinifrons extremus*; New Guinea); 1969: 206 (*Psenulus extremus*).

New records from NE. New Guinea: 1 ♀, East Highlands Aiyura, 1800—1900 m, 6 Jan. 1965, J. Sedlacek (BISH); 1 ♂, Huon Gulf, Morobe District, 22 May—19 June 1937, J. L. Froggatt (BM).

The male is slightly paler coloured than the allotype and paratype recorded in 1966. Pronotum, posterior half of scutellum and metanotum brown. Pronotal tubercles yellowish-brown. Fore and mid tibiae entirely yellow. Basal  $\frac{2}{3}$  of hind tibiae yellow in dorsal aspect, also hind basitarsi yellow.

Antennal segments 7—12 with low, yellowish-brown, longitudinal ridge (tyloidea).

### ***Psenulus carinifrons carinifrons* (Cameron)**

Cameron, 1902: 288—289 (*Psen carinifrons*; India).

Van Lith, 1962: 103—104 (*Psenulus carinifrons*); 1966: 43 (*Psenulus carinifrons carinifrons*).

Female (first description). — Length 7 mm. Head and thorax black; scape of antennae yellow, underside of flagellum yellowish-brown. Mandibles yellow with dark red tips. Palpi straw-yellow. Pronotum, pronotal tubercles, scutellum and metanotum yellow. Fore and mid legs including trochanters yellow, tarsi somewhat brownish. Hind trochanters brownish-yellow, femora and tarsi dark brown, tibiae including apical spurs yellow, in lateral view apical  $\frac{1}{5}$  of hind tibiae dark brown. Petiole dark brown, ventral plate, first tergite and second segment except narrow apical margin reddish, rest of gaster blackish-brown. Veins of wings dark brown.

Frons slightly convex, distinctly finely punctate, interstices mostly as large as punctures, vertex still more finely punctate, interstices larger.

Scutum finely punctate, interstices larger than punctures. Scutellum finely sparsely punctate. Back of propodeum smooth behind enclosed area, finely obliquely striate on declivous lateral parts, upper margin of sides with coarse reticulate carination. Mesopleura shining, sparsely punctate.

Pakistan: 1 ♀, Karachi, date in leadpencil indistinct (2.9.03?), T. R. Bell (BM). With note 'out of reedgrass stems; larva feeds on minute froghoppers'.

Two females from Laos are very similar but their gaster is slightly darker. Petiole black, narrow apical margin of ventral plate of petiole reddish. In the female from Tha Ngone the first tergite is dark reddish-brown, second sternite brown, second tergite basally with lateral, round, red mark, hind margin on both sides with narrow reddish mark. Hind trochanters and femora black, hind tibiae yellow, slightly more than apical  $\frac{1}{4}$  black. Length 6.5 mm. In the female from Sayaboury the first tergite is black, base of second tergite laterally with round red mark, slightly more than apical  $\frac{1}{3}$  of hind tibiae black.

Laos: 1 ♀, Vientiane Prov., Tha Ngone, 28 Dec. 1965; 1 ♀, Sayaboury Prov., Sayaboury, 12 Febr. 1966, native collector (BISH).

### ***Psenulus carinifrons rohweri* Van Lith**

Van Lith, 1962: 108 (pro parte; Java, Kangean Is.); 1966: 45; 1969: 205—206 (Luzon, Formosa).

First record from Sumba: 1 ♀, W. Sumba, Kodi, 3 Aug. 1949, Bühler and Sutter (NMB).

The apical third of the hind tibiae is black in dorsal aspect. Hind tarsi including basitarsi dark brown.

### ***Psenulus carinifrons malayanus* Van Lith**

Van Lith, 1969: 206 (Malaya, Singapore, Sumatra, Borneo).

New records from Borneo: 2 ♀, 9 ♂, Sarawak, Kuching, 14 Jan. 1968, C. G. Roche (CGR).

Singapore: 1 ♂, Postal District 17, 17 Jan. 1971, C. G. Roche (CGR).

Malaya: 1 ♀, Penang I., Baker (USNM); 1 ♀, 2 ♂, Perak, Tapah Hill Forest Reserve, 2700 ft, 21 Oct. 1973, C. G. Roche (CGR).

***Psenulus carinifrons scutellatus* Turner**

Turner, 1912a: 54 (*Psenulus? scutellatus*; NE. Australia); 1916: 128 (*Neofoxia scutellatus*).

Van Lith, 1962: 108 (*Psenulus scutellatus*); 1966: 43—44 (*Psenulus carinifrons scutellatus*); 1969: 203—205 (New Guinea, Ambon, Buru, Mindanao); 1970: 103.

New record from Buru: 1 ♀, Station 9, 18 May 1921, L. J. Toxopeus (MA).

***Psenulus sogatophagus* Pagden**

Pagden, 1933: 97—101 (Malaya).

Van Lith, 1966: 42 (Thailand, Assam?)

First records from Laos: 1 ♀, Vientiane Prov., Gi Sion Vill., de Tha Ngone, 24—31 Oct. 1966, native collector; 1 ♂, Sedone Prov., Paksong, 17 May 1965, P. D. Ashlock (BISH).

***Psenulus xanthognathus xanthognathus* Rohwer**

Rohwer, 1910: 660 (*Psenulus (Neofoxia) xanthognathus*; Luzon).

Van Lith, 1962: 104—107 (*Psenulus carinifrons xanthognathus*; Luzon); 1966: 44—45; 1969: 206 (*Psenulus xanthognathus xanthognathus*); 1972: 196.

New records from Luzon: Laguna, 1 ♀, Los Baños, Mt. Makiling, Baker, 1 ♂, Los Baños, Baker (USNM), Laguna, Agricultural College, 2 ♀, 2 ♂, 6 Sept. 1931, F. C. Hadden (BM); 1 ♂, Albay Prov., Libon, Caguscus, 200 m, 12 May 1965, H. M. Torrevillas (BISH); 2 ♂, Mount Prov., Ifugao, Mayoyao, 1000—1500 m and 1200—1500 m, 9 July and 3 Sept. 1966; 3 ♀ and 8 ♂, Rizal, Mt. Montalban, Wawa Dam, 150—200 m, 25 Febr.—19 March 1965, H. M. Torrevillas (BISH).

Antennal segments 5—12 or 6—11 of male with indistinct, low, somewhat shining tyloidea.

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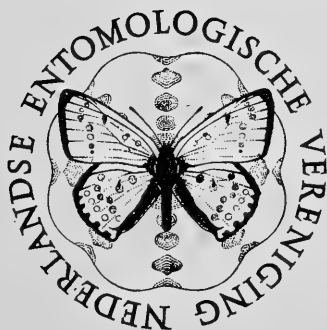
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# ORTHOPTEROIDEA OF CRETE

by

F. WILLEMSE and G. KRUSEMAN<sup>1)</sup>

*With 13 text-figures and ten plates*

## ABSTRACT

Previous records and 3300 newly collected specimens formed the basis of this survey of the Orthopteroidea (= Orthoptera-Saltatoria) of Crete. The following new taxa, all from Crete, are described: *Platycleis* (*P.*) *grisea cretica*, *Eupholidoptera forcipata*, *E. latens*, *E. pallipes* and *E. gemellata*. The following species are new to the fauna of Crete: *Phaneroptera n. nana* Fieber, *Homorocoryphus n. nitidulus* (Scopoli), *Sepiana sepium* (Yersin), *Heteracris l. littoralis* (Rambur) and *Tropidopola longicornis* (Fieber) (ssp.n.?). The occurrence of *Platycleis* (*P.*) *escalerai* I. Bolívar could be confirmed. However, previous records of *Acrometopa servillei* (Brullé), *Eupholidoptera chabrieri* (Charpentier), *Troglophilus cavicola* (Kollar), *Omocestus petraeus* (Brisout), and *Oedipoda miniata* (Pallas) are considered unreliable. In all, at least 63 species are listed. The typically insular fauna of Crete is closely related to the fauna of the Cyclades and the southern Sporades, while the relationship between Crete and Anatolia appears to be closer than that between Crete and the Greek mainland. Besides, there exists an affinity to the Sicilian fauna, although apparently less close than to the fauna of the eastern part of the Mediterranean Region.

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## INTRODUCTION

The latest survey of the Orthopteroidea of Crete was given by Ramme (1927). The present authors, together with their families, collected new material (3300 specimens), from 44 localities, which served as a basis for the present critical study. About half of this material has been deposited in the Instituut voor Taxonomische Zoölogie, University of Amsterdam, while the other half, including the

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types of the new taxa, is preserved in the collection of the senior author.

References given under the species names usually concern records of original material. As to the localities of the species, the reader is referred to the map (Fig. 13). Each locality or group of adjacent localities has been given a number, which refers to the "List of Localities", p. 155. The list contains the data on the localities visited recently as well as those of previous records, as far as traceable.

The classification of the higher taxa of the Acridomorpha in the present paper is that of Dirsh (1975).

The collecting of additional material from another 13 localities by the following persons is gratefully acknowledged here: A. C. & W. N. Ellis, Amsterdam; W. H. Gravestijn, Amsterdam; J. A. W. Lucas, Rotterdam; S. J. van Ooststroom; Oegstgeest; J. H. Woudstra, Zaandam; valuable information was provided by A. Kaltenbach, Vienna and D. K. McE. Kevan, Quebec.

#### LIST OF SPECIES FOUND ON CRETE

- |   |  |
|---|--|
| <i>Phaneroptera n. nana</i> Fieber                  | <i>T. roeweri</i> Werner                                 |
| <i>Tylopsis lilifolia</i> (Fabricius)               | <i>Gryllus bimaculatus</i> De Geer                       |
| <i>Acrometopa cretensis</i> Ramme                   | <i>Acheta domesticus</i> (Linné)                         |
| <i>Poecilimon cretensis</i> Werner                  | <i>Tartarogryllus bordigalensis</i> (Latreille)          |
| <i>Conocephalus (Xiphidion) discolor</i>            | <i>Modicogryllus geticus</i> Vasiliu (?)                 |
| Thunberg  | <i>Gryllomorpha dalmatina</i> (Ocskay)                   |
| <i>Homorocoryphus n. nitidulus</i> (Scopoli)        | <i>G. cretensis</i> Ramme                                |
| <i>Tettigonia viridissima</i> (Linné)               | <i>Discoptila lindbergi</i> Chopard                      |
| <i>Decticus albifrons</i> (Fabricius)               | <i>Arachnocephalus vestitus</i> Costa                    |
| <i>Platycleis (P.) grisea cretica</i> subspec. nov. | <i>Myrmecophilus (Myrmophilina) ochraceus</i> Fischer    |
| <i>P. (P.) intermedia</i> (Serville)                | <i>Trigonidium cicindeloides</i> Rambur                  |
| <i>P. (P.) affinis</i> Fieber                       | <i>Oecanthus pellucens</i> (Scopoli)                     |
| <i>P. (P.) escalerae</i> I. Bolívar                 | <i>Gryllotalpa gryllotalpa</i> (Linné)                   |
| <i>P. (Incertana) incerta</i> Brunner v.W.          | <i>Tetrix depressa</i> (Brisout)                         |
| <i>Sepiana sepium</i> (Yersin)                      | <i>Paratettix meridionalis</i> (Rambur)                  |
| <i>Eupholidoptera astyla</i> (Ramme)                | <i>Paranocarodes fieberi</i> (Brunner v.W.)(?)           |
| <i>E. cretica</i> Ramme                             | <i>Orchamus raulinii</i> (Lucas)                         |
| <i>E. forcipata</i> spec. nov.                      | <i>O. y. yersini</i> (Brunner v.W.)(?)                   |
| <i>E. latens</i> spec. nov.                         | <i>Pyrgomorpha c. conica</i> (Olivier)                   |
| <i>E. pallipes</i> spec. nov.                       | <i>Tropidopola longicornis</i> (Fieber) (subspec. nov.?) |
| <i>E. gemellata</i> spec. nov.                      | <i>Calliptamus italicus</i> (Linné)                      |
| <i>Rhacocleis germanica</i> (Herrich Schaeffer)     | <i>C. b. barbarus</i> (Costa)                            |
| <i>Uromenus (Bolivarius) elegans</i> (Fischer)      | <i>Heteracris l. littoralis</i> (Rambur)                 |
| <i>Dolichopoda paraskevi</i> Boudou-Saltet          | <i>Pezotettix giornae</i> (Rossi)                        |
| <i>D. spec.</i> Boudou-Saltet                       | <i>Anacridium aegyptium</i> (Linné)                      |
| <i>Troglophilus spinulosus</i> Chopard              | <i>Ochrilidia pruinosa</i> Brunner v.W.                  |
|   | <i>O. tibialis</i> (Fieber)(?)                           |

<i>Dociostaurus maroccanus</i> (Thunberg)	<i>A. t. thalassinus</i> (Fabricius)
<i>Chorthippus (Glyptobothrus) b. brunneus</i>	<i>Acrotylus l. longipes</i> (Charpentier)
(Thunberg)	<i>A. patruelis</i> (Herrich Schaeffer)
<i>C. (G.) biroi</i> (Kuthy)	<i>A. insubricus inficitus</i> (Walker)
<i>Truxalis nasuta</i> (Linné)	<i>Oedipoda caerulescens</i> (Linné)
<i>Locusta migratoria</i> Linné	<i>O. venusta</i> Fieber
<i>Oedaleus decorus</i> (Germar)	<i>Sphingonotus spec.</i>
<i>Aiolopus strepens</i> (Latreille)	<i>Acrida turrita</i> (Linné) (?)

## SYSTEMATIC PART

Tettigonioidea  
Tettigoniidae  
Phaneropterinae

***Phaneroptera nana nana* Fieber, 1853**

Localities. N. Réthimnis: 49 (1 ♀).

Distribution. *P. nana* is distributed throughout the Mediterranean Region, western Arabia, Africa and Madagascar. The range of the nominate subspecies covers the northern part of this area, coinciding almost exactly with the Mediterranean type of vegetation and Mediterranean crops.

Discussion. Recently *P. nana sparsa* Stål has been found in Spain (Ragge, 1965). It should be noted here that the comparative length of the fore wing and hind femur of our specimen agrees with the nominate subspecies and not with *sparsa*.

Up to now not recorded from Crete.

***Tylopsis lilifolia* (Fabricius, 1793)**

*Tylopsis lilifolia*: Werner, 1903: 68; Kuthy, 1907: 553; Werner, 1927: 428; Ramme, 1927: 188.

Localities. N. Chaníou: 9 (1 ♀); 15e (1 ♂); 16 (1 ♂ 1 ♀); 17b (Werner, 1927), c (1 ♂ 1 ♀); 20 (1 ♂); 22b (Kuthy, 1907); 31 (2 ♂ 2 ♀); N. Réthimnis: 40 (1 ♂ 1 ♀); 41 (1 ♂ 1 ♀); 46 (Kuthy, 1907); 49 (2 ♀); 50b (1 ♀); 56 (3 ♀); N. Irákliou: 61 (2 ♂ 1 ♀); 63 (2 ♂ 1 ♀); 65 (2 ♂); 69 (1 ♂); 71a (2 ♀), d (3 ♂ 3 ♀); 74 (1 ♂); 83a (Werner, 1903); 97a (1 ♀); N. Lassithíou: 107b (1 ♂); 116 (2 ♂); 118 (Ramme, 1927); 122e (1 ♀).

Distribution. The range of this species covers most of the Mediterranean Region.

***Acrometopa cretensis* Ramme, 1927**

*Acrometopa macropoda*: Kuthy, 1907: 553 (misidentification).

*Acrometopa servillea*: Werner, 1927: 428 (misidentification?).

*Acrometopa cretensis* Ramme, 1927: 122, Fig. 5e-8e, Pl. f. 5b-c.

Localities. N. Chaníou: 6a (Ramme, 1927); 13 (1 ♀); 19 (Werner, 1927) ?; N. Réthimnis: 46 (Kuthy, 1907; Ramme, 1927); N. Iráklíou: 71a (1 ♀); 97a (1 ♂); N. Lassithíou: 118 (Ramme, 1927); 120 (Ramme, 1927).

Distribution. This species is known from Crete and some islands of the Cyclades: Kímolis, Polívos, Íos, Antíparos, Kýthnos and Kéa (Werner, 1934, 1937).

Discussion. *A. servillea* has been recorded only once from Crete (Werner, 1927, referring to a juvenile male). Most probably the specimen belongs to *cretensis*, which was described shortly after Werner's paper had been published. For the time being, we remove *servillea* from the faunistic list of Crete.

### **Poecilimon cretensis** Werner, 1903

*Poecilimon jonicus cretensis* Werner, 1903: 67, Fig.

*Poecilimon distinguendus* Kuthy, 1907: 554.

*Poecilimon cretensis*: Ramme, 1927: 186; Harz, 1969: 137, Fig. 292—293, 323, 418—419.

Localities. N. Chaníou: 1 (1 ♂); 13 (2 ♂); 22d (1 ♂); N. Réthimnis: 38a (Werner, 1903); 52b (Kuthy, 1907); 53 (93 ♂ 43 ♀); 54a (Kuthy, 1907), b (Ramme, 1927); N. Iráklíou: 71a (31 ♂ 24 ♀); 78 (Ramme, 1927); 83b (3 ♂ 4 ♀); 86c (Kuthy, 1907); 91 (Kuthy, 1907); 93 (Ramme, 1927); N. Lassithíou: 107a (Ramme, 1927); 118 (Ramme, 1927); 127 (Harz, 1969); 128 (Ramme, 1927).

Distribution. Known only from Crete and one island of the Cyclades: Náxos (Ramme, 1927).

Discussion. This species occurs from the lowlands up to above the timberline (2200 m, 52b). Specimens from above the present-day timberline show extensive black pigmentation.

### **Conocephalinae**

#### **Conocephalus (Xiphidion) discolor** Thunberg, 1815

*Niphidium* [sic] *fuscum*: Kuthy, 1907: 553.

Localities. N. Chaníou: 22b (Kuthy, 1907); N. Iráklíou: 71b (1 ♀), d (10 ♂ 13 ♀ 2 juv.).

Distribution. This species is found in the British Isles and throughout Europe, extending into Palaearctic Asia and N. Africa.

#### **Homorocoryphus nitidulus nitidulus** (Scopoli, 1786)

Localities. N. Réthimnis: 41 (1 juv.).

Distribution. This species is widely spread throughout the southern part of Europe, in subtropic and tropical Africa, and in Palaearctic Asia.

Discussion. Up to now not recorded from Crete.



## Tettigoniinae

**Tettigonia viridissima** (Linné, 1758)

*Tettigonia viridissima*: Werner, 1927: 428; Ramme, 1927: 188.

Localities. N. Chaníou: 1 (1 juv.); 15e (4 ♂ 2 ♀); 26b (Werner, 1927); N. Iráklíou: 71a (1 ♂ observed); 78 (Ramme, 1927); N. Lassithíou: 121 (Ramme, 1927).

Distribution. This species occurs in most of the Palaearctic Region.

## Decticinae

**Decticus albifrons** (Fabricius, 1775)

*Decticus (Locusta) albifrons*: Lucas, 1854: 167.

*Decticus albifrons*: Werner, 1903: 68; Ramme, 1927: 188.

Localities. N. Chaníou: 10 (Lucas, 1854); N. Réthimnis: 38a (Werner, 1903); 40 (1 ♀); 49 (4 ♂ 1 ♀); 50b (1 ♂); N. Iráklíou: 71d (1 ♂ 1 ♀); 86a (Lucas, 1854); N. Lassithíou: 111b (Ramme, 1927); 112 (Ramme, 1927).

Distribution. The range of this species covers the Mediterranean Region and extends into southwestern Asia.

**Platycleis (Platycleis) grisea cretica** subsp. nov.

(Pl. 1 Fig. 2, Pl. 2 Fig. 5)

The material from Crete was compared with over 300 specimens of the *grisea*-complex, originating from more than 50 localities (lowland up to 2200 m) and representing nominate *grisea* (Fabricius), *grisea transiens* Zeuner, including topotypes of the latter, and *grisea monticola* Chopard. Special attention was given to specimens from the high mountains of Greece.

The *grisea* material, except for that from Crete, is characterized as follows: elytron more than three times as long as pronotum (from 3.2 to 5.1 times), even if elytron does not reach hind knee completely; Rs vein (nomenclature as proposed by Ragge, 1955) distinctly separated from MA and with some accessory posterior branches; exceptionally, Rs fused with MA for a short distance, but then these veins distinctly diverging again apically; elytron strongly elongate, anterior and posterior margins roughly parallel, apex widely rounded; hind wing hardly shorter than elytron, MA with a number of accessory posterior branches; hind femur invariably slender, distinctly attenuate apically.

As to the characters of the tegmina and the hind femur, it is apparent that the material from Crete (Pl. 1 Fig. 2, Pl. 2 Fig. 5) and that from Greece (Pl. 1 Fig. 1, Pl. 2 Fig. 4) is different (compare a study on *Platycleis (Tessellana)* by Kaltenbach, 1964). However, the abdominal terminalia and the superficially studied stridulatory apparatus appear to be similar. We consider the population of Crete to belong to the *grisea*-complex but to represent a distinct subspecies.

Material studied: ♂ holo-, ♀ allo-, 5 ♂ 9 ♀ paratypes, labelled: Hellas, Kriti, Idi Oros, Kolita-Psiloritis 1700-2100 m, 28-29. vii. 1973; additional paratypes: Lefka Ori, Linoseli above Xiloskalo 1800-1900 m, 5.viii. (1 ♀) & Omalos 1000 m, 4.viii. (1 ♂ 2 ♀) 1973, all F. Willemse c.s.

### Description.

♂, ♀ (Pl. 1 Fig. 2, Pl. 2 Fig. 5). Within the *grisea*-complex distinct by shorter tegmina and hind femur. Elytron not or slightly extending beyond tip of abdomen, by far not reaching hind knee, not more than 2-3 times as long as pronotum; basally, including the stridulatory apparatus in the male, as wide as usual; apically strongly narrowing towards narrowly rounded or subacute apex; R vein divided into R1 and Rs, bifurcation located as usual; Rs after a short distance completely fused with MA (in 18 specimens) or nearly touching MA (in 2 specimens); elimination of the area between Rs and MA, together with shortening of the longitudinal veins and reduction of the areas posteriorly of R, results in brachyptery. Hind wing short, only slightly longer than half the elytron; MA without accessory branches, area between MA and MP strongly reduced. Hind femur comparatively short, slightly attenuate apically. Male cercus of usual shape, slightly shorter than in nominate *grisea*. Epiphallus as in *grisea*-complex. Female abdominal terminalia about as in *grisea transiens*, hind margin of last abdominal sternite more or less elevated in the middle. Coloration as usual.

Measurements (length in mm). Idi Oros (6 ♂ 10 ♀): body ♂ 17.0-18.1, ♀ 17.3-19.0; pronotum ♂ 5.1-5.9, ♀ 5.2-5.6; elytron ♂ 10.6-12.7, ♀ 10.3-12.8; hind femur ♂ 14.8-15.1, ♀ 13.9-15.4; ovipositor 9.9-10.8; Linoséli (1 ♀): body 17.1; pronotum 5.6; elytron 13.1; hind femur 15.8; ovipositor 10.3; Omalos (1 ♂ 2 ♀): body ♂ 17.2, ♀ 17.6-17.9; pronotum ♂ 5.0, ♀ 5.2-5.5; elytron ♂ 14.2, ♀ 14.8-15.0; hind femur ♂ 15.1, ♀ 16.1-16.9; ovipositor 10.1-10.2.

Localities. N. Chaníou: 13; 15e; N. Réthimnis: 53.

Distribution. Known only from the western and central mountains of Crete.

Discussion. The available material is uniform as to its general appearance. The tegmina and the hind femora of the few specimens from Omalos are slightly longer (1-3 mm) than those of the specimens from above the timberline, which differences may be connected with differences in altitude. The venation and the shape of the tegmina are uniform, except for the course of Rs in both elytra of the male from Omalos and in the right elytron of the female from Linoséli. In these elytra Rs and MA are separate, although very close, almost touching each other.

Galvagni (1959) described an other short-winged form in *Platycleis* (*Platycleis*), viz., *P. (P.) concii*. This species occurs in the Madonie mountains of Sicily, from 1000 up to 1800 m altitude. Comparison of *concii* (Pl. 1 Fig. 3, Pl. 2 Fig. 6) with *grisea cretica* reveals the shape and venation of the tegmina to be nearly the same. However, the long and attenuate hind femur, the more robust general appearance with wider head and thorax and the larger measurements in the former are quite distinct.

Previous records of *grisea* from Crete are doubtful: Griffini (1894: 92) records a single male from Láki (17a) and Ramme (1927: 188) a single male from Ierápetra (111b). Both records probably refer to *intermedia*. Distinction between the males

of *grisea* and *intermedia* was hardly possible in the time of Griffini's paper, nor in that of Ramme's. Reliable records of *intermedia* (based on the female) from the two localities are now available: from Ierápetra by Ramme himself (1951), and from Láki in the present material. We assume that the only representative of the *grisea*-complex in Crete is *grisea cretica*.

Details of the localities and the habitat of *grisea cretica* are discussed below under *Eupholidoptera forcipata* and *pallipes*. Flight was not observed.

### **Platycleis (Platycleis) intermedia (Serville, 1839).**

*Platycleis grisea*: Griffini, 1894: 92 (misidentification ?); Ramme, 1927: 188 (idem).

*Platycleis intermedia*: Kuthy, 1907: 553; Ramme, 1951: 245, 247.

Localities. N. Chaníou: 15b (Kuthy, 1907); 16 (2 ♂); 17a (Griffini, 1894) ?, c (2 ♀); 31 (6 ♂ 3 ♀); N. Réthimnis: 40 (2 ♀); 46 (Kuthy, 1907); 48 (4 ♂ 3 ♀); 49 (1 ♂ 4 ♀); 50b (1 ♂ 5 ♀); 55 (1 ♂); N. Iráklíou: 61 (1 ♀); 71a (2 ♂); 90c (1 ♂ 1 ♀); 91 (Kuthy, 1907); 97a-b (11 ♂ 1 ♀); N. Lassithíou: 108 (1 ♂); 109 (1 ♀); 111a (Ramme, 1951), b (Ramme, 1927) ?; 119 (2 ♀); 122d (1 ♀).

Distribution. The range of this species covers S. Europe and N. Africa, and extends far into Palaearctic Asia.

Discussion. Previous records of *grisea* by Griffini and Ramme which are here referred to *intermedia*, are discussed under *grisea cretica*. It should be noted here that the specimens of *intermedia* from Crete usually are smaller than those from the mainland of Europe, and thus resemble *grisea* (especially the male).

### **Platycleis (Platycleis) affinis Fieber, 1853**

*Platycleis affinis*: Werner, 1903: 68.

Localities. N. Réthimnis: 40 (1 ♀); 50b (2 ♂ 5 ♀); N. Iráklíou: 86b (Werner, 1903).

Distribution. This species occurs in central, but mainly in southern Europe, extending into northern Africa and far into western Asia.

### **Platycleis (Platycleis) escalerae I. Bolívar, 1899**

*Platycleis escalerae* (?): Ramme, 1927: 143, 188.

Localities. N. Iráklíou: 61 (2 ♂ 2 ♀); 71d (1 ♀); N. Lassithíou: 111b (Ramme, 1927).

Distribution. This species is distributed throughout southeastern Europe and the adjacent part of western Asia.

Discussion. While Ramme was not certain of his identification of a single male from Ierápetra, the present material is proof of the occurrence of this species in Crete.

### **Platycleis (Incertana) incerta Brunner von Wattenwyl, 1882**

*Incertana incerta*: Zeuner, 1941: 37, Fig. 31.

Localities. Crete (Zeuner, 1941); N. Chaníou: 15e (1 ♂ 3 ♀); 16 (1 ♂); 31 (2 ♂); N. Réthimnis: 40 (1 ♂ 1 ♀); 41 (9 ♂ 2 ♀); 48 (1 ♂ 1 ♀); 49 (2 ♂); 50b (3 ♂ 2 ♀); 56 (2 ♀); N. Iráklíou: 57 (4 ♂); 61 (1 ♀); 63 (1 ♂); 71d (18 ♂ 24 ♀).

Distribution. Known from the Balkan peninsula, Crete, some Aegean islands and Turkey.

### *Sepiana sepium* (Yersin, 1854)

Localities. N. Réthimnis: 40 (1 ♀); 50b (1 ♂ 1 ♀); N. Iráklíou: 71d (2 ♂ 2 ♀).

Distribution. The range of this species covers southern Europe, including some Mediterranean islands, and extends into Turkey.

Discussion. Up to now not recorded from Crete.

### *Eupholidoptera* Ramme, 1951

Up to now, two species of *Eupholidoptera* were known from Crete. In the present material another four, apparently new, species are recognized. The following descriptions of the new species were made after comparison with the type-species, *E. chabrieri* (Charpentier).

#### Key to the males of the *Eupholidoptera* species from Crete

1. Cercus and subgenital plate with teeth . . . . . 2
- Cercus and subgenital plate without teeth . . . . . 3
2. Tip of epiphallus with a lateral spine on each side (Pl. 7 Fig. 35—36) . . . . .  
     . . . . . *pallipes* spec. nov.
- Tip of epiphallus laterally rounded and without spines (Pl. 7 Fig. 37—38) . . . . .  
     . . . . . *gemellata* spec. nov.
3. Stylus of subgenital plate long, about as long as cercus (Fig. 7); epiphallus symmetrical, apical parts close together, partly fused (Fig. 9) . . . . . *cretica* Ramme
- Stylus of subgenital plate short, shorter than half length of cercus; epiphallus asymmetrical, or if symmetrical, then with apical parts divergent . . . . . 4
4. Median excision of hind margin of subgenital plate very wide and deep and more than half the length of the plate (Pl. 5 Fig. 21); epiphallus symmetrical, large, robust, apical parts divergent (Pl. 6 Fig. 29—31) . . . . . *forcipata* spec. nov.
- Median excision less wide and deep . . . . . 5
5. Hind margin of last abdominal tergite with a narrow median excision (Fig. 1); epiphallus asymmetrical, apical parts partly fused (Fig. 4) . . . . . *astyla* (Ramme)
- Hind margin with a wider median excision (Pl. 5 Fig. 19); epiphallus symmetrical, apical parts divergent (Pl. 7 Fig. 32—34) . . . . . *latens* spec. nov.

A key to the females of *Eupholidoptera* from Crete is not given. Distinctive characters are apparent only in *forcipata*, while the females of *cretica* and *gemellata* are unknown.

Kuthy (1907: 553) recorded *Thamnotrizon chabrieri* from Amari (46). Ramme (1927: 194) briefly discussed this record, but Kuthy's material could not be traced.

As to the range of this species, its occurrence in Crete is not probable and confirmation is needed. For the time being, the species is omitted from the faunal list of Crete.

***Eupholidoptera astyla* (Ramme, 1927)**  
(Fig. 1—5)

*Pholidoptera astyla* Ramme, 1927: 133, 196, 198, Fig. 11d, 13—14; Ramme, 1930: 799, 821, Fig. 5—7, 9; Ramme, 1939: 94—96, 100, Fig. 27.

*Eupholidoptera astyla*: Ramme, 1951: 198, 203, 206, 209, 211, Fig. 51; Harz, 1969: 362, 377, Fig. 1109, 1130, 1159—1161.

Localities. N. Lassithíou: 107a; 111b; 112 (all Ramme, 1927).

Distribution. This species is known only from the original material: a male from Náxos (the Cyclades), and three females and the tip of a male abdomen from eastern Crete. The male from Náxos has been selected as lectotype. Therefore Náxos is the type-locality and not Crete, as indicated by Harz (1969).

***Eupholidoptera cretica* Ramme, 1951**  
(Fig. 6—9)

*Eupholidoptera cretica* Ramme, 1951: 198, 202, 203, 211, Fig. 47, 51; Harz, 1969: 362, 377, Fig. 1111—1112.

Localities. N. Chaníou (12b) (Ramme, 1951).

Distribution. The species is known only from the male holotype. As far as could be traced, Sanmaria, in the original description, was a misspelling of Samariá.

***Eupholidoptera forcipata* spec. nov.**

(Pl. 2 Fig. 7—8, Pl. 4 Fig. 14, Pl. 5 Fig. 18, 21, Pl. 6 Fig. 25, 29—31, Pl. 8 Fig. 39)

Material studied: ♂ holotype, ♀ allotype, 45 ♂ and 59 ♀ paratypes, labelled: Hellas, Kriti, Idi Oros, Kolita-Psiloritis 1700-2100 m, 28-29.vii.1973, F. Willemse c.s.

**Description.**

♂ (Pl. 2 Fig. 7). Robust. Pronotum wide, scarcely or not widening posteriorly, metazona comparatively short, hind margin slightly convex. Legs short and thick.

Last abdominal tergite (Pl. 5 Fig. 18) curved strongly downwards; hind margin with a deep and wide median excision, which is transversely concave in the middle and straight at sides; from this excision, at either side, projects a large, triangular lobe with slightly wrinkled surface and strongly toothed apex, which points ventro-laterally.

Cercus (Pl. 6 Fig. 25) without tooth, short, about as long as last abdominal tergite measured in the middle; basal half roughly cylindrical and straight, apical half narrowing at inner side and slightly upcurved, apex obtusely pointed.

Subgenital plate (Pl. 5 Fig. 21) without spines, very large, slightly wider than long and slightly tapering apically, distal half strongly slanting upwards and, in

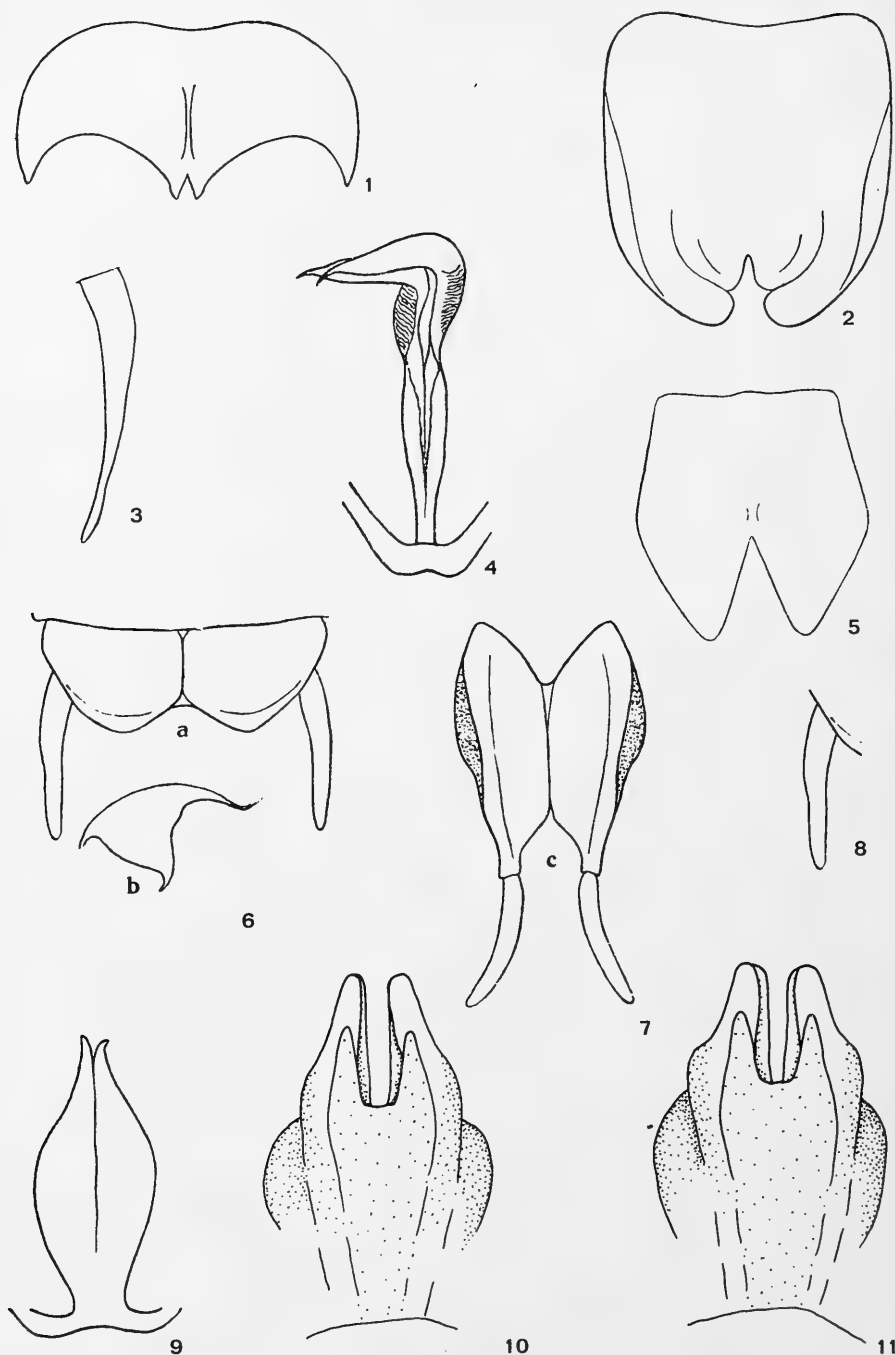


Fig. 1—5. *Eupholidoptera astyla* (Ramme). 1—4, male; 1, last abdominal tergite; 2, subgenital plate; 3, cercus, dorsal view; 4, epiphallus; 5, female, subgenital plate. Fig. 6—9, *E. cretica* Ramme, male. 6, last abdominal tergite; 7, subgenital plate; 8, cercus, dorsal view; 9, epiphallus. (All after Ramme). Fig. 10—11. *Tropidopola longicornis* (Fieber) subsp. nov.?, apex of phallus of two males from Amnissós

closed position, covering distal part of last abdominal tergite; anterior margin with an obtuse-angled excision; posterior margin very wide, with a deep and rectangular excision; lateral parts of plate angularly bent dorsad along a low and smooth lateral ridge from which the stylus arises distally. Stylus short, not exceeding one fourth of cercal length, about two or three times as long as wide.

Epiphallus (Pl. 6 Fig. 29—31) strongly sclerotized, large; apical parts fused and narrow in proximal half, strongly divergent, hook-like and recurved in distal half, extending far over last abdominal tergite.

General colour yellowish brown. Clypeus, frons and genae with several symmetrically arranged black points. Vertex and occiput with a pair of black, medial fasciae, composed of transverse stripes and usually separated from each other by a yellow median line. Above the eye a longitudinal black stripe, behind the eye a similar but wider one. Pronotal dorsum, in middle of prozona, with black markings in varying degree, metazona sometimes with green flush. Pronotal lateral lobe with wide, black, dorsal fascia, in prozona not sharply delimited ventrally, in metazona sharper and strongly narrowing posteriorly. Elytron and last abdominal tergite completely black. First abdominal tergite partly black, other abdominal tergites faintly dotted with dark brown. Abdominal sternites orange brown, subgenital plate orange yellow, the latter with lateral parts black. Cercus dark brown. Fore and middle legs with numerous black points and stripes. Hind femur with a short, longitudinal, black stripe dorso-basally, usually composed of a series of transverse stripes; outer side with a large, roughly triangular or V-shaped black streak near the middle and with more or less numerous blackish or dark brownish transverse stripes. Apical half of hind femur with a short, dorsal, black stripe. Hind knee and postgenicular part of hind tibia black, except dorsally.

♀ (Pl. 2 Fig. 8). Slightly larger than male. Elytron almost completely covered by pronotum. Cercus very slightly curved upwards, short, conical, apex pointed. Abdominal sternites simple. Subgenital plate (Pl. 8 Fig. 39) much wider than long, distal half strongly slanting upward; posterior margin slightly converging towards a deep but narrow median excision, which reaches at least middle of plate and has the angles widely rounded. Ovipositor comparatively short, straight or slightly curved upwards apically. Coloration as in male.

Measurements (length in mm): body ♂ 21.0—24.0, ♀ 18.5—24.0; pronotum ♂ 9.2—10.1, ♀ 9.0—9.2; elytron ♂ 5.4—6.5, ♀ 3.0—4.0; hind femur ♂ 15.4—16.9, ♀ 17.0—17.6; ovipositor 16.0—17.2.

Localities. N. Réthimnis: 53.

Distribution. Known only from Mt. Idi, central Crete.

Discussion. *E. forcipata* is well characterized by its abdominal terminalia and close to *anatolica* (Ramme). In the male of the latter species the posterior margins of the last abdominal tergite and that of the subgenital plate are excised in a much different way, while the stylus is more elongate and the proximal half of the apical parts of the epiphallus is wider.

The type-locality, Kolita-Psiloritis, can be reached by foot from Kamáres (520 m), a village on the southeastern slopes of Mt. Idi. From there a track follows the main water-pipe of the village and leads to several springs. The last and highest of these springs is named Skaroneró (1650 m) and is the type-locality

of *E. gemellata* (see below). At a short distance and after passing the present-day timberline, a small plateau with some shepherd's huts is reached, named Kolíta (1750 m). During the night spent up there we experienced considerable night-frost. *E. forcipata* was mainly collected in the surroundings of the huts. It lives rather hidden in low, dense, prickly shrubs, e.g. *Astragalus* spec., and is found together with *Poecilimon cretensis* and *Platycleis grisea cretica*. The collecting was considerably facilitated by the use of firm gloves. At times the sound of *E. forcipata* was heard, during the warmest hours of the day. As in most of *Eupholidoptera* species, the sound much resembles that of *Ephippiger* species.

***Eupholidoptera latens* spec. nov.**

(Pl. 3 Fig. 9—10, Pl. 4 Fig. 15, Pl. 5 Fig. 19, 22, Pl. 6 Fig. 26, Pl. 7 Fig. 32—34, Pl. 8 Fig. 40)

Material studied: ♂ holotype, ♀ allotype, 2 ♂ 3 ♀ paratypes, labelled: Hellas, Kriti, Lefka Ori, refuge near Koukoule 1600-1800 m, 6.viii.1973; additional paratypes: 1 ♂, Lefka Ori, Linoséli above Xiloskalo, 1800-1900 m, 5.viii.1973, and 1 ♂, Lefka Ori, Omalos, 1000 m, 4.viii.1973, all F. Willemse c.s.

**Description.**

♂ (Pl. 3 Fig. 9). Pronotum with metazona comparatively short, posterior margin slightly convex.

Last abdominal tergite (Pl. 5 Fig. 19) strongly curved downwards; posterior margin with a wide, concave, moderately deep, median excision, which is sharply toothed laterally, the teeth pointing ventrally.

Cercus (Pl. 6 Fig. 26) without tooth, long, about twice as long as last abdominal tergite (measured in the middle), slender; basally almost three times as wide as apically, slightly curved inward; apex obtusely pointed.

Subgenital plate (Pl. 5 Fig. 22) without spines, much longer than wide, strongly tapering distally; distal part slanting upwards, in closed position scarcely covering last abdominal tergite; ventral surface with median keel; lateral margin bent upwards proximally, strongly inflated distally and there forming a smooth, wide range, ridges on either side converging towards apex of plate; apex with narrow, triangular, median excision, which does not reach farther than one-fourth of length of plate. Stylus (Pl. 4 Fig. 15) short and thick, length about one-fifth of cercus, straight, cylindrical, about two or three times as long as wide, inserted pre-apically at ventral surface of subgenital plate and pointing ventrally (i.e. perpendicularly to the subgenital plate).

Epiphallus (Pl. 7 Fig. 32—34) strongly sclerotized, of moderate length, apical parts fused and wide in proximal half, moderately divergent, hook-like and weakly recurved in distal part; the latter extends over last abdominal tergite.

Coloration as in *forcipata*, but black markings, especially those of hind femur, less conspicuous.

♀ (Pl. 3 Fig. 10). Slightly larger than male. Elytron completely covered by pronotum or almost so. Cercus straight, short, conical, apex pointed. Abdominal sternites simple. Subgenital plate (Pl. 8 Fig. 40) about as long as wide; posterior



margin obliquely convergent towards a triangular, median excision, which reaches about one-third of length of plate, its posterior angles narrowly rounded. Ovipositor slightly curved apically. Coloration as in male.

Measurements (length in mm): body ♂ 18.0-23.0, ♀ 17.8-18.2; pronotum ♂ 8.7-9.4, ♀ 8.2-8.5; elytron ♂ 4.5-6.0, ♀ 1.0-2.0; hind femur ♂ 16.0-17.5, ♀ 16.1-16.9; ovipositor 13.5-14.4.

Localities. N. Chanfou: 13; 14; 15e.

Distribution. Known only from the Lefka Range, western Crete.

Discussion. This species is well characterized by the abdominal terminalia of the male, and is easily distinguished from the other species of the genus, with the exception of *astyla*. The peculiar position of the male styli resembles that of *astyla*. The latter species differs from *latens*, in the male sex, in the smaller excision of the posterior margin of the last abdominal tergite (Fig. 1), the more inwards curved cercus (Fig. 3), the less tapering subgenital plate (Fig. 2), and the quite distinct epiphallus (Fig. 4). Distinction of *latens* and *astyla* in the female sex is not obvious. The slight differences in shape of the subgenital plate (Fig. 5, Pl. 8 Fig. 40) cannot be considered reliable, as the variation in both species is insufficiently known.

The type-locality can be reached, by car, from the village and high plateau, both named Omalós (1000 m). Via a rather bad track of about 5 km, a refuge „Kalérji” belonging to the Hellenic Alpine and Ski Federation is reached. It lies close to one of the peaks of the Lefka Range, named Koukoulé. The specimens were sparsely found in the surroundings of the refuge, where they live remarkably hidden in dense shrubs, e.g. *Juniperus*. Catching them appeared to be a rather exhaustive task. The adjacent locality Linoséli is discussed below under *E. pallipes*. *E. latens* also occurs on the slopes bordering the Omalós plateau, where it lives in shrubs of *Quercus coccifera*, and again is very difficult to find. Using its song, which much resembles that of *Ephippiger*, as a guide, only one single male could be caught during twilight.

A single female from Mt. Idi, found above Kamáres (1000 m) on our way to Kolíta (see under *E. forcipata*), much resembles *latens*. However, without the male, we are not certain as to its true identity.

### ***Eupholidoptera pallipes* spec. nov.**

(Pl. 3 Fig. 11—12, Pl. 4 Fig. 16, Pl. 5 Fig. 20, 23, Pl. 6 Fig. 27, Pl. 7 Fig. 35—36, Pl. 8 Fig. 41)

Material studied: ♂ holotype, ♀ allotype, 5 ♂ paratypes, labelled: Hellas, Kriti, Lefka Ori, Linoséli above Xiloskalo, 1600—1800 m, 5.viii.1973, F. Willemse c.s.

### **Description.**

♂ (Pl. 3 Fig. 11). Eyes prominent. Pronotum not widening posteriorly; lateral edges of dorsum widely rounded; metazona very short, with slightly flattened dorsum and without median keel or almost so; posterior margin slightly convex.

Last abdominal tergite (Pl. 5 Fig. 20) moderately curved downwards; posterior strongly produced apically with a narrow, roughly rectangular or heart-shaped

median excision, which is strongly toothed laterally, teeth pointing towards each other or more to the ventral side.

Cercus (Pl. 6 Fig. 27) of moderate length, about as long as last abdominal tergite; relatively thick, basally twice as wide as apically, slightly curved inwards, with a narrow, inwards curved, inner tooth at short distance from basis; apex of cercus obtusely pointed, apex of tooth sharply spined.

Subgenital plate (Pl. 5 Fig. 23) about as in the type-species; longer than wide, moderately tapering distally, in closed position not covering last abdominal tergite; posterior margin with a moderately deep and narrow, concave, median excision and, at either side, a single spine situated between median excision and insertion of stylus. Stylus as in the type-species, at least half as long as cercus.

Epiphallus (Pl. 7 Fig. 35—36) weakly sclerotized, narrow and long; apical parts completely fused along whole length, slightly recurved, slightly tapering distally but tip widening again and, at either side, with a fine lateral spine; apical parts considerably projecting, reaching level of apex of cerci.

General colour pale yellow brown. Frons above clypeal margin with a pair of large black spots, which may be fused into a single transverse fascia. Vertex of general colour, occiput and area along dorsal margin of eye completely black. Pronotum of general colour, or, usually, with small black spot in central part of metazona of lateral lobe. Elytron and abdomen as in the type-species. Legs unicolorous, hind femur without black markings, hind knee sometimes blackish.

♀ (Pl. 3 Fig. 12). Elytron completely covered by pronotum. Cercus curved slightly inwards, short, conical, apex pointed. Subgenital plate (Pl. 8 Fig. 41) as long as wide, hind margin slightly convergent towards a wide, concave, median excision, which reaches about one-fourth of length of plate, its apical angles widely rounded. Ovipositor slightly curved apically. Coloration as in male.

Measurements (length in mm): body ♂ 18.0-21.0, ♀ 16.0; pronotum ♂ 7.4-7.9, ♀ 7.5; elytron ♂ 3.8-5.0, ♀ 1.5; hind femur ♂ 14.0-15.0, ♀ 16.5; ovipositor 15.0.

Localities. N. Chaníou: 13.

Distribution. Known only from the Lefka Range, western Crete.

Discussion. The species is well characterized by the external abdominal terminalia, which resemble those of the type-species, together with the unique epiphallus of the male and the rounded pronotum and unicolorous legs in both sexes.

The type-locality is accessible by foot from a refuge named Xilóskalo (1200 m), situated at the southernmost point of the Omalós plateau. From here a mountain track in the direction of one of the peaks of the Lefka Range, named Gigilós (2080 m), leads to a spring and saddle both named Liñoséli. The latter is the precise locality of the type-series. The habitat is similar to that of *forcipata*. The song has not been heard.

#### ***Eupholidoptera gemellata* spec. nov.**

(Pl. 4 Fig. 13, 17, Pl. 5 Fig. 24, Pl. 6 Fig. 28, Pl. 7 Fig. 37—38)

Material studied: ♂ holotype, labelled: Hellas, Kriti, Idi Oros, Kamares-Kolita, Skaronero 1650 m, 28.vii.1973, F. Willemse c.s.

**Description.**

♂ (Pl. 4 Fig. 13). Resembling *pallipes*, but epiphallus distinct. Apical parts of epiphallus (Pl. 7 Fig. 37—38) not fused along their whole length; distal thirds separated, although close together and wider; tip simply rounded without lateral spines.

Coloration differing from *pallipes* in black spots on pronotum, which are larger and fused over the pronotal dorsum into a single, wide, transverse black band, and also in the absence of black spots on frons.

♀. Unknown.

Measurements (length in mm): body 18.0; pronotum 7.5; elytron 3.2; hind femur 16.0.

Locality. N. Iráklíou: 67.

Distribution. Known only from Mt. Idi, central Crete.

Discussion. The single available specimen lacks the left hind leg and the left fore leg is slightly deformed. Although much resembling *pallipes*, the different shape of the epiphallus justifies its specific distinction. The differences in the male cercus (Pl. 6 Fig. 27—28) in *pallipes* and *gemellata* should not be considered reliable, as variation in both species is insufficiently known.

The type-locality is described under *E. forcipata*. The specimen was found on *Quercus coccifera*, about 15 m above the spring.

### **Rhacocleis germanica (Herrich-Schaeffer, 1840)**

*Rhacocleis germanica*: Ramme, 1927: 188; Uvarov, 1942: 312.

Localities. N. Chaníou: 12a (Uvarov, 1942); 17c (2 ♂); 20 (1 ♀); 31 (1 ♀); 35d (2 ♂ 2 ♀); N. Réthimnis: 40 (1 ♀); 44a (Ramme, 1927); 49 (2 ♂ 7 ♀ 2 juv.); 50b (1 ♀); N. Iráklíou: 71d (1 ♀); 74 (1 ♂ 1 ♀); 86e (Uvarov, 1942).

Distribution. The range of this species extends from southern France to southern Slovakia, Moldavia and western Turkey. It is known from Corsica, Sicily, Kerkyra (= Corfu) and Crete, but not from the other Aegean islands.

### **Ephippigerinae**

#### **Uromenus (Bolivarius) elegans (Fischer, 1853)**

*Ephippigera idomenaei* Lucas, 1854: 165, Pl. 2 Fig. 1; Werner, 1903: 68, Fig.; Kuthy, 1907: 553.

*Steropleurus siculus*: Ramme, 1927: 188.

*Steropleurus idomenaei*: Uvarov, 1942: 320, Pl. 26 Fig. 31.

Localities. N. Chaníou: 10 (Lucas, 1854); 12a (Uvarov, 1942); 31 (2 ♂ 2 ♀); N. Réthimnis: 38a (Werner, 1903); N. Iráklíou: 69 (1 ♂); 71a (1 ♂ 3 ♀); 72 (Ramme, 1927); 86a-b-c (Lucas, 1854; Werner, 1903; Kuthy, 1907); 83a (Werner, 1903); 90b (1 ♂); 97b (2 ♂); N. Lassithíou: 106 (Ramme, 1927); 107a (Ramme, 1927); 109 (1 ♀); 111b (Ramme, 1927); 113 (Ramme, 1927); 119 (1 ♂); 120a (Ramme, 1927); 126 (Ramme, 1927).

Distribution. The range of this species covers the mainland of Italy (from Toscana to Calabria), while it also occurs on the islands Corsica, Elba, Giglio, Sardegna, Sicily and Crete.

Grylloidea  
Rhaphidophoridae  
Dolichopodinae

**Dolichopoda paraskevi** Boudou-Saltet, 1973

*Dolichopoda* spec. Chopard, 1957: 26. (? partim)

*Dolichopoda paraskevi* Boudou-Saltet, 1973: 58, Fig. A-K.

Distribution. Recorded only from the type-locality: N. Iráklíou: 92a-b (Chopard, 1957 ?; Boudou-Saltet, 1973).

**Dolichopoda spec.** Boudou-Saltet, 1973

*Dolichopoda* spec. Boudou-Saltet, 1973: 59, Fig. L-N.

Distribution. Known only from the type-locality: N. Lassithíou: 102b. This species was described but not yet named by lack of a male.

**Dolichopoda spec.** Chopard, 1957

*Dolichopoda* spec. Chopard, 1957: 26; Boudou-Saltet, 1973: 57.

Localities. N. Lassithíou: 98a-b & 99a-b (Chopard, 1957; Boudou-Saltet, 1973). Specimens from caves, which have not been identified due to their juvenile stage.

Troglophilinae

**Troglophilus spinulosus** Chopard, 1921

*Troglophilus spinulosus* Chopard, 1921: 147, Fig.; Chopard, 1957: 26.

Localities. N. Chaníou: 5a (Chopard, 1957); 23a (Chopard, 1957), c (Chopard, 1957); N. Réthimnis: 37b (Chopard, 1921); N. Lassithíou: 102a (Chopard, 1957).

Distribution. Known only from Crete.

Discussion. The species was described after a juvenile male. The precise type-locality is unknown, and placed tentatively under 37b.

**Troglophilus roeweri** Werner, 1927

*Troglophilus roeweri* Werner, 1927: 429, Fig. 1—2, 6; Chopard, 1957: 26.

Distribution. Known only from the type-locality: N. Chaníou: 23d.

Discussion. The record of *Troglophilus cavicola* from Chaniá (22a) in Werner

(1903: 69) refers, according to that author (1927: 429), to *spinulosus* or *roeweri*. According to Chopard (1957: 26) both names could be synonymous.

### **Troglophilus spec.**

*Troglophilus*: Boudou-Saltet, 1973: 57.

Localities. N. Chaníou: 4; 5b; 15f; 23a-b-c; N. Lassithíou: 102b (all Boudou-Saltet, 1973).

Discussion. This record refers to a list of caves from which *Troglophilus* is known without further specification.

### **Gryllidae**

### **Gryllinae**

### **Gryllus bimaculatus De Geer, 1773**

*Liogryllus bimaculatus*: Ramme, 1927: 189.

Localities. N. Chaníou: 24 (Ramme, 1927); 28c (Ramme, 1927); N. Réthimnis: 50b (2 ♀); N. Iráklíou: 68 (1 ♀); 97b (5 juv.).

Distribution. The range of this species covers southern Europe and extends into Africa and Asia.

### **Acheta domesticus (Linné, 1758)**

*Gryllus domesticus*: Ramme, 1927, 189.

Localities. N. Chaníou: 33 (Ramme, 1927); N. Réthimnis: 54b (Ramme, 1927).

Distribution. Occurring throughout most of the world.

### **Tartarogryllus bordigalensis (Latreille, 1804)**

*Gryllus bordigalensis*: Kuthy, 1907: 553; Ramme, 1927: 189.

Localities. N. Chaníou: 22b-c (Kuthy, 1907; Ramme, 1927).

Distribution. This species is distributed throughout the Mediterranean Region, its range extending into western Asia.

### **Modicogryllus geticus Vasiliu, 1970**

*Gryllus algericus*: Kuthy, 1907: 553. (?)

Locality. N. Chaníou: 22b (Kuthy, 1907).

Distribution. Known from Roumania, Yugoslavia and European Turkey.

Discussion. Kuthy's record probably refers to *algericus* Brunner von Wattenwyl, 1882 (nec Saussure), which was described by Kis (1967) under the name *chopardi*. The latter name being preoccupied, it has been changed into *geticus*. Confirmation is needed, especially because Kuthy's material might belong to another species of this genus, for instance *algerius* (Saussure).

**Gryllomorpha dalmatina** (Ocskay, 1832)

*Gryllomorpha dalmatina*: Werner, 1927: 431; Chopard, 1957: 28.

Localities. N. Chaníou: 18 (Werner, 1927); N. Lassithíou: 102a (Chopard, 1957).  
Distribution. The range of this species covers the Mediterranean Region.

**Gryllomorpha cretensis** Ramme, 1927

*Gryllomorpha cretensis* Ramme, 1927: 189.

Localities. N. Réthimnis: 44 (Ramme, 1927); N. Iráklíou: 57 (1 ♀).

Distribution. Known only from Crete.

Discussion. This species was known only from its type-specimen (♀). Our adult specimen agrees with Ramme's description, except for the coloration of the head, which is not unicolorous. The vertex between the eyes and the fastigium are dark brown, while the occiput, genae and face are much paler. The measurements (length in mm) are as follows: body 9.6; pronotum 1.6; hind femur 6.0; hind tibia 4.5; ovipositor 6.4.

**Discoptila lindbergi** Chopard, 1957

*Discoptila lindbergi* Chopard, 1957: 26, Fig. 1, 3.

Localities. N. Iráklíou: 58a-b; 60; 88; N. Lassithíou: 98a; 99a, c; 102a; 115 (all Chopard, 1957).

Distribution. Known only from Crete.

**Mogoplistinae****Arachnocephalus vestitus** Costa 1855

*Arachnocephalus vestitus*: Kuthy, 1907: 554.

Localities. N. Chaníou: 22b (Kuthy, 1907); N. Iráklíou: 57 (1 ♀); 65 (1 ♀).

Distribution. This species occurs in the Mediterranean Region.

**Myrmecophilinae****Myrmecophilus (Myrmophilina) ochraceus** Fischer, 1853

*Myrmecophila ochracea*: Kuthy, 1907: 554; Ramme, 1927: 190.

Localities. N. Chaníou: 3 (Ramme, 1927); N. Iráklíou: 86c (Kuthy, 1907); N. Lassithíou: 122f (2 ♀).

Distribution. The range of the species covers the Mediterranean Region.

**Trigonidiinae****Trigonidium cicindeloides** Rambur, 1839

*Trigonidium cicindeloides*: Kuthy, 1907: 553; Ramme, 1927: 189.

Localities. N. Chaníou: 8 (1 ♀); 22b (Kuthy, 1907); N. Iráklíou: 71c (1 ♂ 7 juv.); N. Lassithíou: 120a (Ramme, 1927).

**Distribution.** Widely distributed in the Mediterranean Region, Asia, Africa and Madagascar.

### Oecanthinae

#### **Oecanthus pellucens** (Scopoli, 1763)

*Oecanthus pellucens*: Kuthy, 1907: 553; Ramme, 1927: 189.

**Localities.** N. Chaníou: 15b (Kuthy, 1907); 16 (1 ♀); 22b (Kuthy, 1907); N. Réthimnis: 56 (1 ♀); N. Iráklíou: 57 (1 ♀); 84 (3 ♀); 85b (1 ♀); 90b (1 ♂); 97b (1 ♀); N. Lassithíou: 121 (Ramme, 1927); 122e (1 ♀).

**Distribution.** The range of this species covers central Europe, the Mediterranean Region and N. Africa.

### Gryllotalpoidea

#### Gryllotalpidae

#### **Gryllotalpa gryllotalpa** (Linné, 1758)

*Gryllotalpa vulgaris cophtha*: Werner, 1903: 69.

*Gryllotalpa vulgaris*: Kuthy, 1907: 554; Ramme, 1927: 190.

*Gryllotalpa gryllotalpa*: Werner, 1927: 431.

**Localities.** N. Chaníou: 19 (Werner, 1927); 22b (Kuthy, 1907); N. Réthimnis: 47b (Werner, 1903).

**Distribution.** Widely spread throughout Europe, northern Africa and Asia.

**Discussion.** The locality Kolomodis, recorded by Ramme (1927), could not be traced and is omitted from our list of localities.

### Tetrigoidea

#### Tetrigidae

#### Tetriginae

#### **Tetrix depressa** (Brisout, 1848)

*Tetrix depressus*: Kuthy, 1907: 552.

**Locality.** N. Chaníou: 22b (Kuthy, 1907)

**Distribution.** The range covers the Mediterranean Region and extends far into Palaearctic Asia.

#### **Paratettix meridionalis** (Rambur, 1838)

*Paratettix meridionalis*: Kuthy, 1907: 552; Ramme, 1927: 190.

**Localities.** Nordküste (Ramme, 1927); N. Chaníou: 22b (Kuthy, 1907); N. Réthimnis: 50b (4 ♂ 5 ♀); N. Iráklíou: 69 (4 ♀ 2 juv.); 83c (9 ♂ 15 ♀ 1 juv.); 86c (Kuthy, 1907); N. Lassithíou: 117 (1 ♂).

Distribution. This species is distributed throughout the Mediterranean Region, extending into western Asia.

Acridomorphaeidea

Pamphagoidea

Pamphagidae

Pamphaginae

**Paranocarodes fieberi** (Brunner von Wattenwyl, 1882)

*Paranocarodes fieberi*: Ramme, 1951: 283.

Discussion. This species has only been recorded once (Ramme, 1951), referring to a female labelled: Kreta, Frivaldsky. Further details on the specimen are not given. Demirsoy (1973) distinguishes several subspecies in *fieberi*, from Turkey. His study deals only with Anatolian material and that from the Aegean islands is not discussed. The occurrence in Crete needs confirmation.

**Orchamus raulinii** (Lucas, 1854)

*Acinipe raulinii* Lucas, 1854: 167, Pl. 2 Fig. 2.

*Pamphagus raulinii*: Brunner von Wattenwyl, 1882: 201; Kuthy, 1907: 553.

*Pamphagus yersinii*: Werner, 1903: 67 (misidentification?).

*Orchamus raulinii*: Ramme, 1927: 192; Uvarov, 1942: 347; Descamps & Mounassif, 1972: 254; Harz, 1975: 109, Fig. 256, 275, 363—364, 367, 371, 384—391.

Localities. N. Chaníou: 15a (Werner, 1903) ?; 24 (Ramme, 1927); N. Réthimis: 54a (Kuthy, 1907; Ramme, 1927); N. Iráklíou: 86a (Lucas, 1854); N. Lassithíou: 122g (Harz, 1975).

Distribution. So far known only from Crete.

Discussion. The types being lost, Harz selected neotypes from Sitía (122g). However, his neotypes should be disregarded because their designation does not agree with Article 75 of the International Code of Zoological Nomenclature. According to Ramme (1927), Werner's record of *yersini* refers to *raulinii*.

**Orchamus yersini yersini** (Brunner von Wattenwyl, 1882)

*Porthetis raulinii* (nec Lucas, 1854): Yersin, 1860: 529, Pl. 10 Fig. 26—28.

*Pamphagus yersini* Brunner von Wattenwyl, 1882: 200.

*Orchamus yersini*: Ramme, 1927: 192; Uvarov, 1942: 347; Ramme, 1951: 411; Descamps & Mounassif, 1972: 252, Fig. 10—11; Harz, 1975: 108, Fig. 267, 276, 365—366, 369—370, 372—375.

Locality. "Candia" (Brunner von Wattenwyl, 1882; Ramme, 1951; Descamps & Mounassif, 1972; Harz, 1975).

Distribution. The nominate subspecies is recorded from Crete, some Aegean



islands (Kós; Marathókampos, Sámos; Kárpáthos), but mainly from Syria and the Lebanon. The subspecies *hebraeus* Uvarov, 1942, is known from Israel.

Discussion. The record from Crete is based on the locality labels of the ♂ holotype and ♀ allotype: Candia, Prof. Zeller, don. Dohrn 1855. However, it is astonishing that since Brunner's record of 1882 or the year of the locality label, 1855, no further material from Crete has become available. An explanation was given by Uvarov (1942) who assumed that the types bear not the correct locality labels and thus *yersini* does not occur in Crete. It is not within the scope of the present paper, to unravel this problem. In any case, confirmation of the occurrence of *yersini* in Crete is needed.

## Pyrgomorphidae

### Pyrgomorphinae

#### *Pyrgomorpha conica conica* (Olivier, 1791)

*Pyrgomorpha grylloides*: Griffini, 1894: 92; Werner, 1903: 67; Kuthy, 1907: 553; Ramme, 1927: 192.

Localities. N. Chaníou: 20 (27 ♂ 16 ♀); 22b (Kuthy, 1907); 25a (Griffini, 1894); N. Réthimnis: 38a (Werner, 1903); 54b (Ramme, 1927); N. Iráklíou: 71a-b (8 ♂ 13 ♀); 73 (Ramme, 1927); 74 (1 ♀); 76 (Ramme, 1927); 78 (Ramme, 1927); 81 (1 ♀); 83a (Werner, 1903); 85a-b-c (3 ♂ 7 ♀); 86c (Kuthy, 1907), d (Ramme, 1927); 90a-b (2 ♀); 91 (Kuthy, 1907); 93 (Ramme, 1927); N. Lassithíou: 104 (1 ♀); 105b (2 ♂ 2 ♀); 108 (1 ♂); 109 (2 ♂); 111b (Ramme, 1927); 119 (1 ♀); 122b-c (6 ♂ 11 ♀).

Discussion. A revision of *Pyrgomorpha* is currently in progress (Kevan, 1971 and 1974). Mr. Kevan studied a sample of our material and kindly informed us that we are dealing with the nominate subspecies.

## Acridoidea

### Catantopidae

#### Tropidopolinae

#### *Tropidopola longicornis* (Fieber, 1853) subsp. nov. ?

(Fig. 10, 11, Pl. 8 Fig. 42—43)

Localities. N. Iráklíou: 71b (2 ♂ 4 ♀), c (1 ♂), d (1 ♂ 3 ♀, reared to adult stage in October); 84 (3 ♂); 86f (1 ♂); 90b (12 ♂ 10 ♀); N. Lassithíou: 122e (11 ♂ 10 ♀).

Discussion. *Tropidopola* has not yet been recorded from Crete. The latest revision of the Mediterranean species was given by La Greca (1964). He mentioned the following taxa: *cylindrica cylindrica* (Marshall, 1836) from the western Mediterranean area; *graeca graeca* Uvarov, 1926, from mainland Greece, southern and western Anatolia, and Cyprus; *graeca transjonica* La Greca, 1964, from Taranto, Apulia, S. Italy; *longicornis longicornis* Fieber, 1853, from Egypt (type-locality proposed by Uvarov, 1926: 173, which is not in accordance with Fieber's

original data); and *longicornis syrica* (Walker, 1871) from Syria and Palestine. Our material does not fit any of these taxa. The shape of the head (Pl. 8 Fig. 42—43) and of the male cercus resemble *longicornis* rather than *graeca*. The antennae are shorter than in nominate *longicornis* and resemble those of *longicornis syrica*. The longest middle segments are between 1.2 to 1.6 times as long as wide. However, the phallic complex (studied in nine males) differs from that of *longicornis* in the apex which is comparatively more elongate, slender, while the outline of the apical penis valves (in lateral aspect) is from hardly (Fig. 10) to moderately (Fig. 11) sigmoid and not angulate or incised as figured by La Greca (1964: Fig. 37—38). After a study of material from other parts of the Mediterranean Region, it became apparent that, due to insufficient knowledge of the individual variation, some characters are not reliable. We consider the *Tropidopola* population of Crete to constitute a distinct geographical race, allied to nominate *longicornis*.

### Calliptaminae

#### *Calliptamus italicus* (Linné, 1758)

*Caloptenus italicus*: Griffini, 1894: 92 (?); Werner, 1903: 67 (?); Kuthy, 553 (?).

*Calliptamus italicus*: Werner, 1927: 431; Jago, 1963: 320.

*Calliptamus italicus grandis*: Ramme, 1927: 193.

**Localities.** Kriti (Jago, 1963); N. Chaníou: 26b (Werner, 1927); 31 (3 ♀); N. Réthimnis: 48 (3 ♂ 1 ♀); 49 (1 ♂ 5 ♀); 50b (1 ♂ 1 ♀); N. Iráklíou: 61 (1 ♂); 71a (3 ♂ 2 ♀), d (3 ♂ 3 ♀); N. Lassithíou: 106 (Ramme, 1927); 107a (Ramme, 1927); 109 (2 ♂); 111b (Ramme, 1927); 114 (Ramme, 1927); 119 (1 ♂).

**Distribution.** The range of this species covers southern Europe and Turkey, from where it extends into central Asia.

**Discussion.** Griffini (1894), Werner (1903) and Kuthy (1907) mentioned only *italicus* and not *barbarus*. However, the latter species is by far more common in Crete as well as throughout southern Europe, where *italicus* ranks second (cf. Jago, 1963: 320). Therefore their records are not included in the locality list above.

#### *Calliptamus barbarus barbarus* (Costa, 1836)

*Calliptamus siculus*: Ramme, 1927: 193.

*Calliptamus barbarus barbarus*: Ramme, 1951: 311; Jago, 1963: 329, 334.

**Localities (summary).** N. Chaníou: 6; 9; 14—17; 20; 31; N. Réthimnis: 37—40; 44; 48—50; 56; N. Iráklíou: 57; 61; 63—65; 67; 69; 71; 74; 82; 84; 87; 89—90; 96—97; N. Lassithíou: 105—107; 116; 120—122; 124—125.

**Distribution.** Widely distributed throughout the Mediterranean Region, its range extending far into Palaearctic Asia.

**Discussion.** The data of our material of *barbarus* (154 ♂ 205 ♀) agree with Jago's remark that *barbarus* in Crete occurs up to 1700 m. The same can be said of *italicus*, which lives up to 1100 m. In the same paper, Jago mentioned the population of *barbarus* in Crete to have bright orange legs, and "many specimens

show separate inner femoral spots". Our specimens have indeed bright orange inner sides of the hind femora and pale orange hind tibiae, but the inner femoral spots are usually fused.

### Eyprepocneminae

#### **Heteracris littoralis littoralis** (Rambur, 1838)

Localities. N. Chaníou: 20 (1 ♂ 4 juv.); N. Iráklíou: 71a (2 ♂ 1 ♀), d (3 juv.); 74 (48 ♂ 32 ♀).

Distribution. The range of the nominate subspecies covers southern Spain (type-locality), northern, western and eastern Africa, and extends into S.W. Asia.

Discussion. Our material was compared with that from southern Spain. The colour of the hind tibiae and the shape of the male subgenital plate agree with the nominate subspecies rather than with *littoralis similis* (Brunner von Wattenwyl, 1861) or other subspecies. At Pitsídia (74) the species is abundant and lives in the dunes under extremely dry and hot conditions.

Till now not recorded from Crete.

### Catantopinae

#### **Pezotettix giornae** (Rossi, 1794)

*Platyphyma giornae*: Griffini, 1894: 92.

*Pezotettix giornae*: Kuthy, 1907: 553; Ramme, 1927: 193.

Localities. N. Chaníou: 9 (1 ♀); 15b (Kuthy, 1907), e (1 ♂ 2 ♀); 16 (2 ♂ 3 ♀); 17a (Griffini, 1894); 20 (1 ♀); 31 (1 ♀); 36 (Ramme, 1927); N. Réthimnis: 37c (Ramme, 1927); 39 (Ramme, 1927); 40 (3 ♂ 2 ♀); 41 (3 ♂ 3 ♀); 49 (1 ♂ 3 ♀); 56 (4 ♂ 2 ♀); N. Iráklíou: 57 (5 ♂ 2 ♀); 61 (1 ♀); 63 (2 ♂); 65 (1 ♂ 7 ♀); 82 (4 ♂ 8 ♀).

Distribution. Widely distributed in the southern part of central Europe and the Mediterranean Region.

### Cyrtacanthacridinae

#### **Anacridium aegyptium** (Linné, 1764)

*Acridium (Gryllus) lineola*: Lucas, 1854: 169.

*Acridium aegyptium*: Griffini, 1894: 92; Werner, 1903: 67; Kuthy, 1907: 553.

*Anacridium aegyptium*: Werner, 1927: 431; Ramme, 1927: 193.

Localities. N. Chaníou: 2 (Lucas, 1854); 6b (1 ♂ 2 ♀); 21 (Werner, 1903); 22c (Ramme, 1927); 26b (Werner, 1927); 28a-b (Lucas, 1854; Griffini, 1894); 30 (Werner, 1903); 35d (2 ♂ 1 juv.); 36 (Ramme, 1927); N. Réthimnis: 41 (1 juv.); 50b (2 ♂); N. Iráklíou: 57 (1 ♂); 63 (1 juv.); 65 (1 ♀); 71a (1 ♀), d (2 ♂ 2 juv.); 74 (1 juv.); 78 (Ramme, 1927); 83c (1 ♂ 1 juv.); 86a (Lucas, 1854), c.d (Kuthy, 1907; Ramme, 1927), f (1 ♂ 2 ♀); 90b (2 ♂); 97a-b (2 ♀); N. Lassíthiou: 104 (1 ♀); 122a (Lucas, 1854); 123 (1 ♀).

Distribution. The range of this species covers southern Europe, large parts of Africa, and S.W. Asia.

Acrididae  
Gomphocerinae

***Ochrilidia pruinosa* Brunner von Wattenwyl, 1882**

*Ochrilidia pruinosa* Brunner von Wattenwyl, 1882: 92.

*Platypterna pruinosa*: Kuthy, 1907: 552; Ramme, 1927: 191, 194; Salfi, 1931: 284, Fig. 48—57.

Localities. N. Chaníou: 20 (1 juv.); 22b-c (Kuthy, 1907; Ramme, 1927); 35b (6 ♂ 3 ♀), d (1 juv. ♀, reared to adult stage in November); N. Iráklíou: 84 (2 ♂); 85c (4 ♂ 1 ♀ 1 juv.); 89 (10 ♂ 9 ♀ 4 juv.); 90b (1 ♂ 1 ♀); N. Lassíthiou); 123 (2 ♂); 125a (63 ♂ 12 ♀).

Distribution. This species, described from Rhódos, has been recorded from Crete, several islands of the Cyclades and Sporades, Cyprus and Mediterranean E. Turkey.

Discussion. The present material has been compared with a large topotypic series from Rhódos, which agrees fairly well with the descriptions and figures of Brunner von Wattenwyl and Salfi. The black spot on the lower inner lobe of the hind knee is uniformly present in the topotypic material and in material from Crete. However, in the specimens from Crete, the typical pruinose coloration is lacking in both sexes, except for the males from Frángo Kástello (35b), in which it is present although less conspicuous than in the topotypic specimens. Also the proportions of the body, tegmina and legs in the specimens from Crete are slightly more robust than in the topotypes. We are not convinced that the *Ochrilidia* population of Crete is identical with *pruinosa*.

From Crete another species of *Ochrilidia* has been recorded, viz., *tibialis* (Fieber). At present its identity is not traceable, as will be pointed out below.

Some references are given:

*Platypterna tibialis* Fieber, 1853: 98; Ramme, 1927: 194; Salfi, 1931: 255, 322, Fig. 179—181.

*Ochrilidia tibialis*: Brunner von Wattenwyl, 1882: 91, Fig. 22; Werner, 1901: 272; Johnston, 1956: 716; Harz, 1975: 603, Fig. 2169—2178.

Fieber's description is unsatisfactory. The locality reads: „Griechenland. Straube. Fieb.". Brunner von Wattenwyl's description gives some useful details. As to the distribution he recorded: „Vorkommen: Griechenland (Fieb.), Candia (c.m.), Spanien (Mus. Genf.). — Ausserdem in Aegypten und Syrien (c.m.).". Salfi gave a full description and figures of the specimen on which Brunner von Wattenwyl's record "Candia" was based. Salfi presumed this specimen to represent Fieber's type. However, Mr. Kaltenbach (Vienna Museum) kindly informed us (in litt. 17.X.1973): „Unser stark beschädigtes und vielfach zusammengeleimtes Exemplar von *Platypterna tibialis* Fieb. angeblich aus der Coll. Fieber trägt an der Nadel 5 Etiketten mit folgender Beschriftung: 1. 9481. — 2. Coll. Br. v. W. ex Coll. Fieber Kreta. — 3. det. Br. v. W. *Ochrilidia tibialis*. — 4. M. Vienna. — 5. *Platypterna tibialis* Fieb. ♀ — M. Salfi det. Die handgeschriebenen Original-

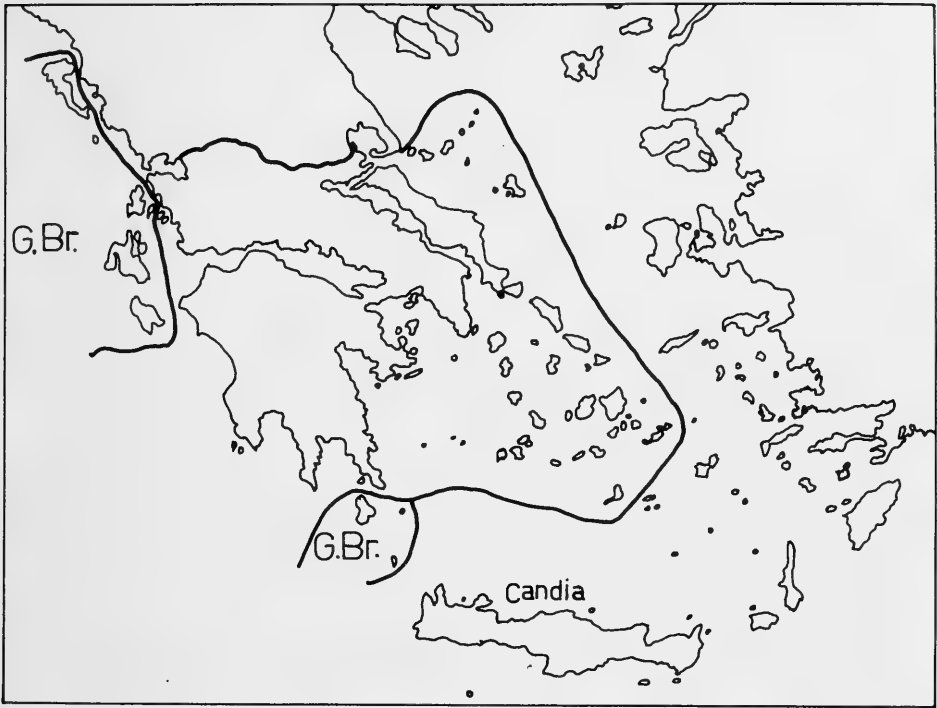


Fig. 12. Greek area in 1850: Greece within the black lines; G. Br., Ionian islands belonging to the United Kingdom; remaining part, Turkey (after A. Stieler, Hand Atlas, Gotha, 1864)

etiketten Brunners (von Fieber ist anscheinend kein Etiket erhalten !) sind in Brunner's Inventar eingeklebt und zeigen die Beschriftung: 1. 9481 *Platypterna*. — 2. *tibialis* Fryvw. 9481 Kreta. „Fryvw.“ steht wahrscheinlich p. err. für „Fieb.“!. Nach dem von Ihnen angegebenen Zitat Brunner's ist es durchaus möglich, dass das Tier Fieber's gar nicht erhalten ist und die gedruckten Etiketten an der Nadel (erst nach dem Tod Brunner's gedruckt) auf Grund eines Missverständnisses den Vermerk „ex Coll. Fieber“ enthalten. In Wirklichkeit handelt es vielleicht um das Tier aus Brunner's eigener Sammlung. Unser ♀ hat helle Kniee wie Salfi angibt. Sonst ist die Art nur durch ein Expl. aus Syrien bei uns vertreten.“

Thus, the validity of the “Kreta” labelled specimen as holotype is at least doubtful. Furthermore, as far as we could trace, additional material which both agrees with Brunner's specimen and originates from Crete or Greece has never more been found since Brunner. Therefore, the occurrence within the region of Greece of an *Ochrilidia* species which lacks the black spots of the lower inner lobe of the hind knee is doubtful. Unless such material will be found and a neotype can be selected, Fieber's *tibialis* is not identifiable. It is pointed out here, that in Fieber's time „Griechenland“ did not cover the actual area of Greece (Fig. 12). Attempts to find out the origin of Fieber's specimen, which he obtained from Straube, a dealer, were not successful.

***Dociostaurus maroccanus* (Thunberg, 1815)**

*Stauronotus maroccanus*: Kuthy, 1907: 552.

*Dociostaurus maroccanus*: Ramme, 1927: 191.

Localities. N. Réthimnis: 54b (Ramme, 1927); 55 (1 ♂); N. Iráklíou: 71a (21 ♂ 28 ♀); 75 (Ramme, 1927); 80 (Ramme, 1927); 86c-d (Kuthy, 1907; Ramme, 1927); 90a (1 ♂ 1 ♀); N. Lassithíou: 105b (3 ♂ 3 ♀); 109 (6 ♂ 1 ♀); 110 (Ramme, 1927); 111b (Ramme, 1927).

Distribution. This species occurs in southern Europe and northern Africa, its range extending far into Palaearctic Asia.

***Chorthippus (Glyptobothrus) brunneus brunneus* (Thunberg, 1815)**

*Stenobothrus bicolor*: Werner, 1903: 67; Kuthy, 1907: 552.

*Stauroderus bicolor*: Werner, 1927: 431; Ramme, 1927: 191.

Localities. N. Chaníou: 11 (Werner, 1903); 15c (Werner, 1927), e (1 ♂); 17b (Werner, 1927); 22b (Kuthy, 1907); N. Réthimnis: 46 (Kuthy, 1907); 54c (1 ♂); 55 (4 ♀); 56 (3 ♂ 10 ♀); N. Iráklíou: 57 (3 ♂ 2 ♀); 64 (1 ♂); 65 (4 ♂ 5 ♀); 83b (1 ♂ 1 ♀); 86c (Kuthy, 1907); 91 (Kuthy, 1907); 97a-b (6 ♂); N. Lassithíou: 105b (1 ♂); 120b (2 ♂).

Distribution. Widely distributed throughout Europe and western Asia.

Discussion. The specimens from Crete are slightly smaller than those from the mainland of Europe and Turkey, and the elytra are slightly less attenuate.

Werner (1903: 66) recorded a male from Chaniá and a male from Réthimnon under *Stenobothrus petraeus* Brisout. His material could not be traced in the Vienna Museum (Kaltenbach, in litt. 8.vii.1975). According to Werner's paper, he had no other material of *petraeus* available. He mentioned that the hind tibiae of these males were yellowish red, which disagrees with his identification. As far as could be traced, there are no further records of *petraeus* from Crete, the Cyclades and the Sporades, nor from the Peloponnese. For the time being, we therefore omit *Omocestus petraeus* (Brisout) from our list.

From Omalós (15), Griffini (1894: 92) recorded a juvenile specimen under *Stenobothrus* spec. ?. From this locality both *brunneus* and *biroi* are known.

***Chorthippus (Glyptobothrus) biroi* (Kuthy, 1907)**

(Pl. 10 Fig. 47—48)

*Stenobothrus biroi* Kuthy, 1907: 552, 554.

*Stauroderus biroi*: Ramme, 1927: 194.

*Chorthippus (Glyptobothrus) biroi*: Harz, 1975: 876, Fig. 3157—3158, 3285—3291.

Localities. N. Chaníou: 9 (2 ♀); 13 (18 ♂ 26 ♀); 14 (5 ♂ 2 ♀); 15b (Kuthy, 1907), e (16 ♂ 10 ♀); 16 (14 ♂ 5 ♀); 17c (1 ♀), d (Harz, 1975); 31 (4 ♂ 4 ♀); N. Réthimnis: 40 (1 ♂); 48 (2 ♂ 3 ♀); 49 (16 ♂ 8 ♀); 50b (1 ♂); 53 (3 ♂ 1 ♀); 56 (2 ♂ 3 ♀); N. Iráklíou: 57 (1 ♀); 65 (3 ♂ 8 ♀); 67 (3 ♂ 1 ♀); 82 (1 ♀); 87 (2 ♂); 90c (3 ♂ 4 ♀); 97b (1 ♂ 3 ♀), c (2 ♂); N. Lassithíou: 101c (Harz, 1975); 116 (4 ♂ 8 ♀); 122d (3 ♂ 1 ♀).

Distribution. So far known only from Crete.

Discussion. This species occurs from lowland up to 2000 m. The shape of the lateral pronotal keels is rather variable. The colour of the hind tibia ranges from pale yellowish to blackish brown. Opportunity is taken here to give some figures of the general appearance of this little known species (Pl. 10 Fig. 47—48).

## Truxalinae

### **Truxalis nasuta** (Linné, 1758)

*Tryxalis procera*: Lucas, 1854: 167 (misidentification?).

*Tryxalis variabilis*: Lucas, 1854: 167.

*Tryxalis unguiculata*: Brunner von Wattenwyl, 1882: 90; Griffini, 1894: 91; Werner, 1903: 66; Kuthy, 1907: 552.

*Acridella variabilis*: Werner, 1927: 431.

*Acridella nasuta*: Ramme, 1927: 190.

*Truxalis nasuta*: Dirsh, 1951: 206, Fig. 139—149, 217, map 9.

Localities. Crete (Dirsh, 1951); Candia (Brunner v.W., 1882); N. Chaníou: 22a-b (Werner, 1903; Kuthy, 1907); 24 (Ramme, 1927); 25a-b (Griffini, 1894; Werner, 1927); 26a-b (Werner, 1927; Ramme, 1927); 28b (Griffini, 1894); 35a (Dirsh, 1951); N. Réthimnis: 37c (Ramme, 1927); 38a-b (Werner, 1903; Ramme, 1927); 46 (Kuthy, 1907); 47a (Griffini, 1894); 54b (Ramme, 1927); N. Iráklíou: 71a-b (1 ♂ 3 ♀); 77 (Ramme, 1927); 83a (Werner, 1903); 85a (1 ♂); 86a-b-c-d (Lucas, 1954; Werner, 1903; Kuthy, 1907; Ramme, 1927); 90a (1 ♂); N. Lassithíou: 104 (1 ♂); 105a (Dirsh, 1951), b (1 ♀); 111b (Ramme, 1927); 112 (Ramme, 1927); 114 (Ramme, 1927); 122b-c (2 ♂).

Distribution. The range of this species covers the southern parts of the mainland of Europe, the Mediterranean islands, and northern Africa, and extends into Palestina and Syria.

Discussion. The record of *procera* Klug, 1830, by Lucas (1854) is most probably erroneous, as Crete is widely separated from the area of distribution of that species (Dirsh, 1951: 183, map 8).

## Oedipodinae

### **Locusta migratoria** Linné, 1758

*Oedipoda Gryllus migratoria*: Lucas, 1854: 170.

*Pachytilus danicus*: Kuthy, 1907: 553.

*Locusta migratoria* ph. *danica*: Ramme, 1927: 191.

Localities. N. Iráklíou: 71d (2 ♂); 86a (Lucas, 1854), c (Kuthy, 1907); N. Lassithíou: 120a (Ramme, 1927).

Distribution. According to Harz (1975: 466) the population of Crete belongs to subspec. *cinerascens* (Fabricius, 1781), which is distributed throughout southern Europe.

**Oedaleus decorus** (Germar, 1826)

*Oedaleus nigrofasciatus*: Werner, 1903: 67.

*Oedaleus decorus*: Ramme, 1927: 191.

Localities. N. Réthimnis: 38a (Werner, 1903); N. Iráklíou: 86b (Werner, 1903), d (Ramme, 1927); 83a (Werner, 1903); N. Lassithíou: 106 (Ramme, 1927).

Distribution. Widely distributed throughout S. Europe, N. Africa and Asia.

**Aiolopus strepens** (Latreille, 1804)

*Epacromia strepens*: Kuthy, 1907: 552.

*Aeolopus strepens*: Ramme, 1927: 191.

*Aiolopus strepens*: Hollis, 1968: Fig. 51.

Localities (summary). N. Chaníou: 15; 17; 22; 34; 36; N. Réthimnis: 37—43; 45; 48; 50; 56; N. Iráklíou: 57; 63; 65; 67; 69; 71; 74; 83—87; 89—90; 97; N. Lassithíou: 105; 107; 117; 122; 125.

Distribution. The range of this common species covers most of the Mediterranean Region.

Discussion. Our material (109 ♂ 96 ♀) was found from the lowland up to 1700 m.

**Aiolopus thalassinus thalassinus** (Fabricius, 1781)

*Oedipoda Acridium laeta*: Lucas, 1854: 170.

*Epacromia thalassinia*: Kuthy, 1907: 552.

*Aeolopus thalassinus*: Ramme, 1927: 191.

*Aiolopus thalassinus thalassinus*: Hollis, 1968: Fig. 84.

Localities. N. Chaníou: 20 (2 ♂); 22b (Kuthy, 1907); 32 (Lucas, 1854); N. Réthimnis: 38b (Ramme, 1927); 50a (2 ♀); N. Iráklíou: 71a-b-c-d (13 ♂ 16 ♀); 84 (1 ♂); 85a (5 ♂ 1 ♀); 86a (Lucas, 1854), d (Ramme, 1927); 90b (2 ♀); 95 (Ramme, 1927); 97b (1 ♂ 1 ♀), d (1 ♀); N. Lassithíou: 108 (1 ♂); 109 (3 ♂); 120b (1 ♂); 122b (3 ♂ 4 ♀), e (2 ♂ 6 ♀).

Distribution. The nominate subspecies occurs in southern Europe, the whole of Africa, its range moreover extending far into southwestern Asia.

Discussion. A record from Mt. Idi (52a) (Lucas, 1854) appears doubtful because the preferred habitat of this species differs very much from that offered by Mt. Idi.

**Acrotylus longipes longipes** (Charpentier, 1843)

*Acrotylus longipes*: Kuthy, 1907: 553.

Localities. N. Chaníou: 20 (4 ♂ 6 ♀); 22b (Kuthy, 1907); N. Iráklíou: 71d (1 ♀); 74 (22 ♂ 19 ♀); 85a (8 ♂), c (13 ♂ 13 ♀); 89 (14 ♂ 14 ♀); 90b (20 ♂ 14 ♀); 97d (21 ♂ 16 ♀).

Distribution. Widely distributed in southeastern Europe, southwestern Asia, and Africa.



**Discussion.** The species lives predominantly along the seashore. The hind wing in our material is yellow or colourless, but not orange.

***Acrotylus patruelis* (Herrich-Schaeffer, 1838)**

*Acrotylus patruelis*: Griffini, 1894: 92; Ramme, 1927: 192.

**Localities.** N. Chaníou: 7 (Ramme, 1927); 13 (1 ♀); 28b (Griffini, 1894); N. Réthimnis: 37c (Ramme, 1927); 42a-b (Ramme, 1927); 43 (Ramme, 1927); 50b (5 ♂ 1 ♀); 56 (2 ♂ 1 ♀); N. Iráklíou: 65 (1 ♂); 71a (2 ♂), d (1 ♂); 87 (1 ♂); 97d (2 ♂ 2 ♀); N. Lassithíou: 104 (1 ♂); 105b (1 ♂); 109 (1 ♂ 1 ♀); 111c (1 ♂ 1 ♀); 177 (1 ♀); 119 (1 ♀); 122d (1 ♂); 125b (1 ♂).

**Distribution.** The range of this species covers the Mediterranean Region, south-western Asia and most of Africa, including Madagascar. In Crete, the species occurs up to 1800 m (13).

***Acrotylus insubricus inficitus* (Walker, 1870)**

*Acrotylus insubricus*: Kuthy, 1907: 552; Ramme, 1927: 192.

*Acrotylus insubricus inficitus*: Mañan, 1958: 177.

**Localities.** Kreta (Mañan, 1958); N. Chaníou: 3 (Ramme, 1927); 20 (1 ♂); 22b (Kuthy, 1907); 24 (Ramme, 1927); 36 (Ramme, 1927); N. Réthimnis: 38b (Ramme, 1927); 39 (Ramme, 1927); 44b (1 ♀); 50b (3 ♂); 51 (Ramme, 1927); N. Iráklíou: 64 (1 ♂); 71d (1 ♀); 75 (Ramme, 1927); 82 (1 ♀); 83c (1 ♂ 1 ♀); 84 (5 ♂ 2 ♀); 85c (1 ♂); 86d (Ramme, 1927), f (1 ♀); 87 (6 ♂ 2 ♀); 89 (2 ♀); 90b (2 ♂), c (5 ♂ 1 ♀); 97c (2 ♀); N. Lassithíou: 116 (3 ♂ 2 ♀); 120a (Ramme, 1927); 124 (1 ♀).

**Distribution.** According to Mañan, this subspecies occurs in central and south-western Asia, the southern part of European USSR, northeastern Africa, and Crete. Our material agrees with his description of the subspecies.

***Oedipoda caerulescens* (Linné, 1758)**  
(Pl. 9 Fig. 44)

*Oedipoda Gryllus caerulescens*: Lucas, 1854: 170.

*Oedipoda caerulea* [sic]: Griffini, 1894: 92.

*Oedipoda caerulescens*: Kuthy, 1907: 553; Werner, 1927: 431; Ramme, 1927: 191.

**Localities (summary):** N. Chaníou: 2; 7; 9; 13—17; 22; 25—28; 31; N. Réthimnis: 37; 39—41; 44; 48—50; 56; N. Iráklíou: 57; 61; 63—65; 67; 69; 71; 74; 82; 86—87; 90; 94; 97; N. Lassithíou: 105; 107; 109—111; 119; 122.

**Distribution.** This species is widely distributed in Europe, northern Africa and western Asia.

**Discussion.** This common species (studied: 148 ♂ 136 ♀) occurs in Crete up to 1800 m. The black fascia of the hind wing, although with a wide overlap, is less strongly developed in the specimens from Crete than in those from the mainland of Greece (Pl. 9 Fig. 44).

***Oedipoda venusta* Fieber, 1853**

(Pl. 10 Fig. 45—46)

*Oedipoda venusta* Fieber, 1853: 23; Brunner von Wattenwyl, 1882: 161; Werner, 1903: 67 (?); Kuthy, 1907: 553; Ramme, 1927: 192; Harz, 1975: 489, Fig. 1615 (*Mioscirtus* v.), 1747.

*Oedipoda gratiosa*: Werner, 1903: 67 (misidentification ?).

Localities. Creta (Brunner v. W., 1882); N. Chaníou: 13 (7 ♂ 6 ♀); 14 (3 ♀); 15b (Kuthy, 1907), e (8 ♂ 5 ♀), g (Harz, 1975); 16 (3 ♂ 4 ♀); N. Réthimnis: 38a (Werner, 1903) ?; 52b (Kuthy, 1907); 53 (16 ♂ 12 ♀); 54a (Kuthy, 1907); 55 (6 ♂ 6 ♀); N. Iráklíou: 67 (11 ♂ 8 ♀); Timbáki, see discussion (Harz, 1975); 83a (Werner, 1903) ?; 94 (Ramme, 1927); N. Lassithíou: 100 (Ramme, 1927); 101b (2 ♀); 103 (Ramme, 1927); 107b (2 ♀); 122c (13 ♂ 13 ♀).

Distribution. Despite Fieber's original record "Griechenland", this species is, as far as known, confined to Crete.

Discussion. The present material agrees with Ramme's comment that the tip of the hind wing in many specimens is but scarcely infusate (Pl. 10 Fig. 45—46). The upper keel of the hind femur is lowered in its apical part, although not as conspicuous as in some other species of *Oedipoda*. Attention is drawn to this character because *venusta* has been placed in some other genera in the older literature (*Scintharista*, *Mioscirtus*, *Microscirtus*, *Morphacris*). This was apparently due to erroneous descriptions, reading in Fieber "Hinterschenkel oben mit ganzem Kiel" and in Brunner von Wattenwyl "femora postica carina superiore haud interrupta".

Among the localities listed above, the name Timbáki refers to: Tympaki, 29.-31.vii.1958, H. Eckerlein (Harz, 1975: Fig. 1747). The locality could no more be included and numbered in the list of localities and on the map, the manuscript being finished.

The male type is damaged and preserved in the Vienna Museum. Harz designated neotypes, which should be disregarded being not in agreement with Article 75 of the International Code of Zoological Nomenclature.

The records of *venusta* and *gratiosa* by Werner (1903) refer to juvenile specimens from the same localities. His material could not be traced in the Vienna Museum (Kaltenbach, in litt. 8.vii.1975). Identification of juvenile specimens in *Oedipoda* species is not reliable. As *gratiosa* (= *miniata* Pallas) has been only recorded once and the record is doubtful, we omit this species from the faunal list of Crete.

***Sphingonotus* spec.**

*Oedipoda Gryllus coeruleans*: Lucas, 1854: 170.

*Sphingonotus caeruleans*: Griffini, 1894: 92.

*Sphingonotus coeruleans*: Kuthy, 1907: 552; Ramme, 1927: 192.

*Sphingonotus rubescens rubescens*: Mistshenko, 1936: 170.

Localities. Crete (Mistshenko, 1936; 3 ♀); N. Chaníou: 9 (1 ♀); 14 (7 ♂ 10 ♀); 15b (Kuthy, 1907), e (16 ♂ 12 ♀); 17c (1 ♂); 20 (2 ♂); 28b (Griffini, 1894); N. Réthimnis: 37a (Lukas, 1854), c (Ramme, 1927); 38b (Ramme, 1927); 42a (Ramme, 1927); 45 (Ramme, 1927); 50b (20 ♂ 14 ♀); 53 (10 ♂ 5 ♀); N. Iráklíou: 67 (6 ♂ 1 ♀); 71a (1 ♂), c (1 ♀); 74 (1 ♀); 79 (Lukas, 1854); 86c-d (Kuthy, 1907; Ramme,

1927); 90a-b (2 ♂ 2 ♀); 93 (Ramme, 1927); 97d (20 ♂ 17 ♀); N. Lassithiou: 101a (Ramme, 1927); 105b (4 ♂ 8 ♀); 108 (2 ♂); 109 (2 ♂ 4 ♀); 111c (1 ♂ 2 ♀); 113 (Ramme, 1927); 120b (2 ♂ 1 ♀); 122b-c-d-e (9 ♂ 11 ♀).

Discussion. *Sphingonotus* is common throughout Crete, from the seashore up to 1800 m. The identification of our material offered considerable difficulties. It agrees partly with *caerulans* (L.) (especially with *caerulans exornatus* Nedelk.), partly with nominate *rubescens* (Walker). However, the greater part of the material is intermediate between these taxa. Especially in longer series from one locality all transitional forms are present. We agree with the critical remarks by Ramme (1951: 406) and abstain from identification of the present material from Crete. We assume that the previous records of *Sphingonotus* from Crete refer to material similar to ours.

### Acridinae

#### *Acrida turrita* (Linné, 1758) (?)

*Tryxalis nasuta* (nec Linné); Kuthy, 1907: 552.

Localities. N. Chaníou: 20 (1 ♂ 1 juv.); 22b (Kuthy, 1907); 35b (1 juv.); N. Réthimnis: 40 (2 juv.); 41 (1 juv.); 50b (1 ♂ 2 juv.); N. Iráklíou: 64 (1 ♀); 71d (2 juv.); 74 (2 juv.); 84 (12 ♂ 7 ♀); 85c (6 ♂ 1 ♀); 86c (Kuthy, 1907); 87 (4 ♂ 1 ♀); 89 (11 ♂ 10 ♀); 90b (9 ♂ 3 ♀); 97c (2 juv.), d (4 ♂).

Distribution. Widely distributed in Africa and recorded from Sicily and Vulcano I.

Discussion. Our material has been identified with the help of the latest revision of the genus (Dirsch, 1954). Judging from the position of the transverse sulcus of the pronotum, which is clearly behind the middle of the pronotum, the population of Crete should belong to *turrita*. However, we are not certain because it is difficult to distinguish it from *bicolor* (Thunberg) (recently synonymized with *ungarica* Herbst), which is the common species of this genus in the Mediterranean Region.

In the older literature there is considerable confusion about the nomenclature in *Acrida* and *Truxalis* species. If the original material cannot be re-examined, old records should be disregarded. However, in this particular case Kuthy's records are interpretable: he recorded both *Tryxalis nasuta* L. and *T. unguiculata* Rambur, which represent *Acrida turrita* (L.) and *Truxalis nasuta* (L.), respectively (compare Brunner von Wattenwyl, 1882: 87—90).

### CONCLUSIONS

Among the present material from Crete, the following new taxa are described: *Platycleis* (*Platycleis*) *grisea cretica* subsp. nov., *Eupholidoptera forcipata*, *E. latens*, *E. pallipes* and *E. gemellata*. As far as we could trace, the following species are new to the fauna of Crete: *Phaneroptera* n. *nana* Fieber, *Conocephalus* (*Xiphidion*) *discolor* Thunberg, *Homorocoryphus* n. *nitidulus* (Scopoli), *Sepiana sepium* (Yersin), *Heteracris* l. *littoralis* (Rambur) and *Tropidopola longicornis* (Fieber) (subsp.

nov.?). The occurrence of *Platycleis (Platycleis) escalerae* Bolívar could be confirmed. The identity of the *Acrida* and *Sphingonotus* material from Crete could not be established.

For various reasons, previous records of *Modicogryllus geticus* Vasiliu, *Paranocarodes fieberi* (Brunner v. W.) and *Orchamus y. yersini* (Brunner v. W.) are doubtful and need confirmation. According to Chopard (1957) *Troglophilus roeweri* Werner could be synonymous with Chopard's *T. spinulosus*. It is pointed out that, for the time being, the identity of *Ochrilidia tibialis* (Fieber) is not clear. Previous records of *Acrometopa servillea* (Brullé), *Eupholidoptera chabrieri* (Charpentier), *Troglophilus cavicola* (Kollar), *Omocestus petraeus* (Brisout) and *Oedipoda miniata* (Pallas) are considered unreliable.

In all, we listed at least 63 species of Orthopteroidea (= Orthoptera-Saltatoria) occurring in Crete. The fauna of Crete is typically insular, i.e. comparatively poor in species. The range of about one third of the species is, as far as known, confined to the island, or covers Crete and some neighbouring islands of the Cyclades. A list of these species is given here:

*Acrometopa cretensis* Ramme  
*Poecilimon cretensis* Werner  
*Platycleis (Platycleis) grisea cretica* subsp. nov.  
*Eupholidoptera astyla* (Ramme)  
*E. cretica* Ramme  
*E. forcipata* spec. nov.  
*E. latens* spec. nov.  
*E. pallipes* spec. nov.  
*E. gemellata* spec. nov.  
*Dolichopoda paraskevi* Boudou-Saltet  
*D. spec.* Boudou-Saltet  
*Troglophilus spinulosus* Chopard  
*T. roeweri* Werner (synon.?)  
*Gryllomorpha cretensis* Ramme  
*Discoptila lindbergi* Chopard  
*Orchamus raulinii* (Lucas)  
*Tropidopola longicornis* (Fieber) subsp. nov. (?)  
*Oedipoda venusta* Fieber  
*Chorthippus (Glyptobothrus) biroi* (Kuthy)

Little can be said about the relationship of these species and subspecies with other members of the genera concerned. The position of *Acrometopa cretensis* is somewhat isolated in the genus, as is discussed by Ramme (1927). The nearest relative of *Poecilimon cretensis* is *P. inflatus* Brunner von Wattenwyl, which occurs in southwestern Anatolia, opposite the southern Sporades. *Platycleis (Platycleis) grisea cretica* comes close to the nominate form and can be considered to be related to the Sicilian species *P. concii* Galvagni. The affinity between the numerous *Eupholidoptera* species is, with few exceptions, far from clear. *Orchamus raulinii* presumably is more closely allied to those species of the genus, which occur in some Aegean islands, Anatolia, Cyprus, Syria, the Lebanon and Israel. Our *Tropidopola* material from Crete comes close to the Egyptian species. *T. longi-*

*cornis* (Fieber), but as pointed out in this paper, a revision of the Mediterranean species is needed and the suggested resemblance with *longicornis* might be incorrect. The relationship with congeneric species in cases like *Oedipoda venusta*, *Chorthippus* (*Glyptobothrus*) *biroi* and the different diverse cave-Orthoptera is doubtful, except for *Dolichopoda paraskevi*. This species comes near *D. naxia* Boudou-Saltet, which occurs in Naxos, one of the Cyclades. This agrees with the close resemblance between the fauna of the Cyclades and that of Crete, which is also proved by the distributional ranges of *Acrometopa cretensis*, *Poecilimon cretensis* and *Eupholidoptera astyla*.

The number of *Eupholidoptera* species confined to Crete is remarkably large, which is very interesting from a zoogeographical point of view. There is a conspicuous difference between the rich fauna of Anatolia and the neighbouring Aegean islands, where the largest number of *Eupholidoptera* species occur, and the poor fauna of the Peloponnese and Kíthira more to the south, which have one species each. This could be an argument that the faunas of Crete and Anatolia would be more closely related than those of Crete and the Peloponnese. However, as to the number of congeneric species, the opposite holds true for *Poecilimon*. While in Crete this genus is represented by one species only (although very close to the Anatolian *P. inflatus*), in Anatolia and the Balkan Peninsula, including the Peloponnese, an overwhelming number of *Poecilimon* species occur.

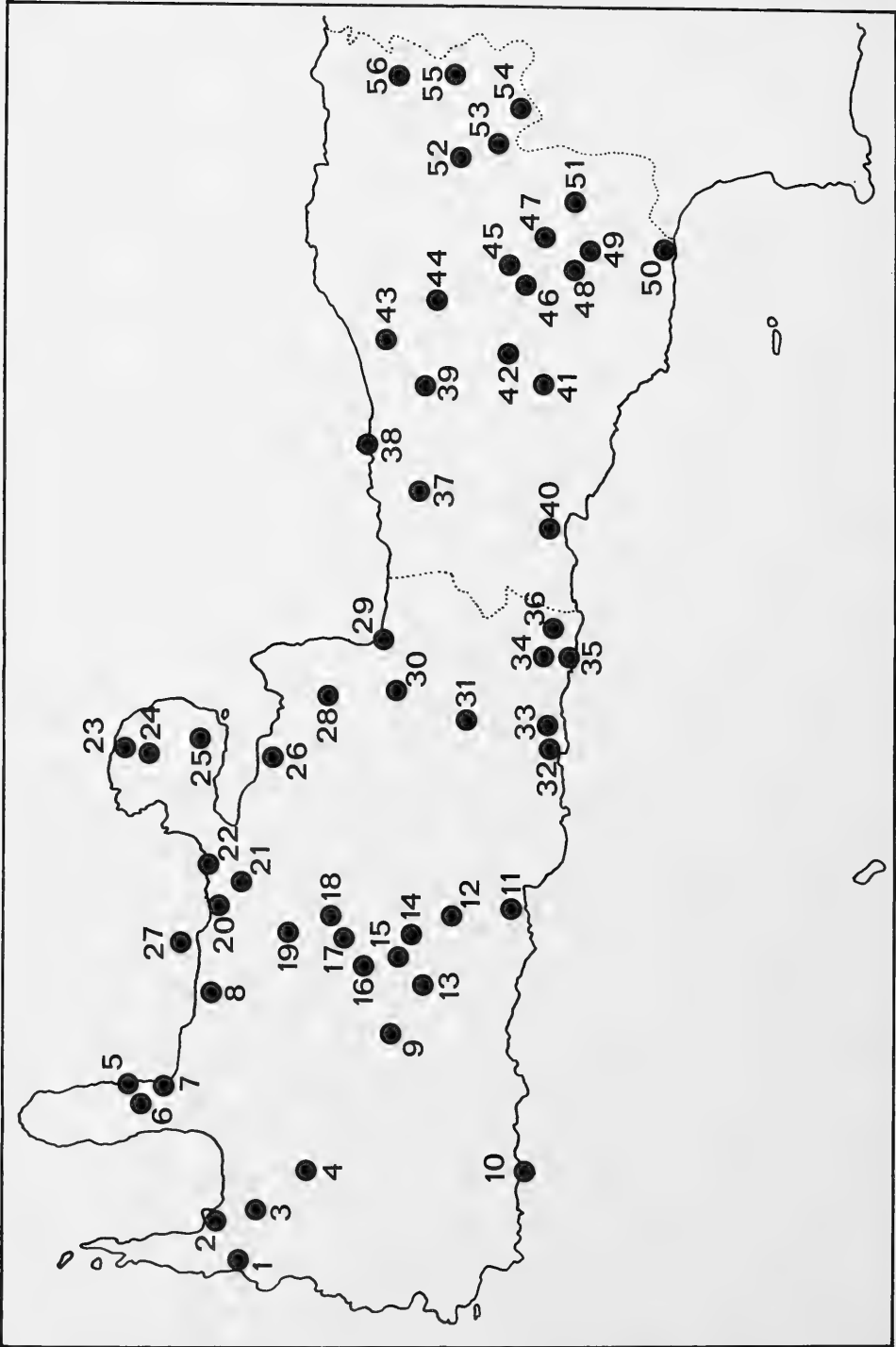
The non-endemic species of Crete are, with few exceptions, widely distributed species: they are found all over the Mediterranean Region, or in its western or eastern parts, or throughout southeastern Europe, including the Peloponnese, the Aegean islands and northwestern Anatolia. A particular case is formed by the only member of the Ehippigerinae in Crete, *Uromenus* (*Bolivarius*) *elegans* (Fischer), which occurs in Corsica, Sardegna, Italy, Sicily and Crete. Actually, Crete forms the southeasternmost part of the range of this subfamily, which has its centre of distribution in southwestern Europe and northwestern Africa. Neither in the Peloponnese, nor in the Aegean islands or Anatolia a member of this subfamily is known to occur. Unfortunately, the distribution in the Greek and Anatolian regions and often the taxonomy of the faunistically more important species are far from sufficiently known.

With so many gaps in our knowledge, it may be clear that only general conclusions can be drawn as to the relationship of the orthopterous fauna of Crete. The closest relationships are found with the fauna of the Cyclades and the southern Sporades. The affinity to the fauna of Anatolia appears to be greater than to that of the Greek mainland, especially of the Peloponnese. Besides there is a resemblance to the fauna of Sicily, although less clear than to that of the eastern part of the Mediterranean Region.

#### LIST OF LOCALITIES

(numbers refer to the map, Fig. 13)

The localities and data of the material studied in the present paper and that recorded previously, are listed below under regional headings: Nomós Chaníou



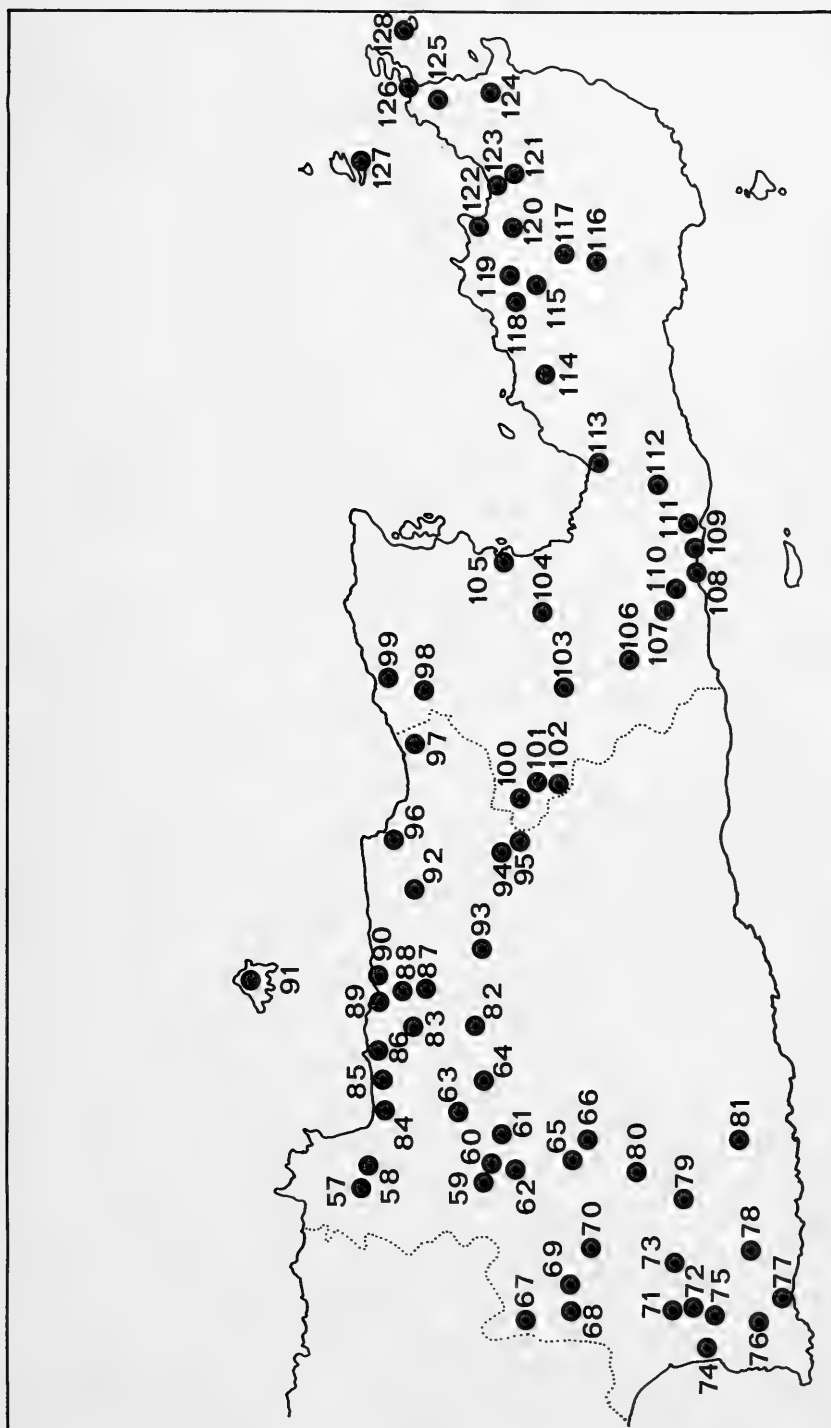


Fig. 13. Map of Crete, numbers refer to List of Localities. A, West Crete; B, East Crete. (Different scales.)

B

nr. 1-36; Nomós Réthimnis nr. 37-56; Nomós Iráklίου nr. 57-97; Nomós Lassithίου nr. 98-128.

The Greek orthography may be transcribed in Roman characters in diverse ways. In our list we use the spelling as printed in the Tourist Map of Crete, copyright Chr. Z. Mathioulakis, Athens. This map is included in H. Guanella, Kreta, Ein Reiseführer, 3. Auflage 1972, Flamberg Verlag, Zürich. Other transcriptions used previously follow the ones used here.

The names of most of the collectors are abbreviated as follows:

(A)	K. Attems	(Li)	K. Lindberg
(B)	L. Biró	(Lu)	J. A. W. Lucas
(C)	G. Cecconi	(Luc)	P. H. Lucas
(B-S)	P. Boudou-Saltet	(S)	A. Schultz
(E)	A. C. & W. N. Ellis	(O)	S. J. van Ooststroom
(Ga)	W. H. Gravestien	(We)	F. Werner
(Ge)	O. Grebenschikoff	(Wi)	F. Willemse c.s.
(K)	M. C. & G. Kruseman	(Wo)	J. H. Woudstra

#### Nomós Chaníou:

1. Falásarna, 7.v.1973 (O & Ga).
2. Kísamos: plateau de Kísamos (Luc).
3. Meráda: Dorf Merades sw. von Kastelli Kisamu, 7.iii.1925 (S).
4. Spília Aghía Sofia: cavité Aghía Sophia, Topolia (B-S).
5. Ellinóspilio,
  - a. Hellinospilo, 25.iv.1955 (Li);
  - b. cavité Hellinospilo (B-S).
6. Rodopóú:
  - a. Rhodopu, 8.x.1926 (S);
  - b. 1.v.1973 (O).
7. Moní Odigitrias: Kloster Gonia, Halbinsel Spatha, 8.x.1925 (S).
8. Geráni, 6.v.1973 (Ga).
9. Vasilianá, 700 m, 7.viii.1973 (Wi).
10. Paleochóra: environs de Séliño (Luc).
11. Aghía Roumeli: Hagia Rumeli, 10.v.1900 (A).
12. Samariá:
  - a. (Ge);
  - b. Sanmaria, 13.vi.1942, Kl. Zimmermann.
13. Linoséli, along mountain track between Xilóskalo and summit Gigilós (Léfka Óri), 1600-1800 m, 5.viii.1973 (Wi).
14. Koukoulé, surrounding of mountain hut "Kalérji" below summit Koukoulé (Léfka Óri), 1600-1800 m, 6.viii.1973 (Wi).
15. Omalós:
  - a. Homalos, 1050 m, 8.v.1900 (A);
  - b. 1050 m, 18.viii.1906 (B);
  - c. Homalos-Ebene, 1000 m, vi.1926 (We);
  - d. 4.v.1973 (Ga);
  - e. Omalós plateau, 1000 m, 4.viii.1973 (Wi);
  - f. grotte Omalos Katavothron (B-S);
  - g. 1000 m, 31.vii.1938 (Ge).
16. Láki-Omalós, between the villages, 750 m, 4.viii.1973 (Wi).



17. Láki:
    - a. Lacus (C);
    - b. Lakkos, in Schluchten, 520 m, vi.1926 (We);
    - c. 450 m, 3.viii.1973 (Wi);
    - d. Lakki, 500-1000 m, 30.vii.1939 (Ge).
  18. Mesklá, Schlucht nach Theriso, 300-540 m, vi.1926 (We).
  19. Fournés: Phurnes, Tal des trockenliegenden Platanos, 100 m, vi.1926 (We).
  20. Makris Tichos, 5 km West of Chaniá, dunes, 0-5 m, 7.viii.1973 (Wi).
  21. Perivolía, südwestlich von Kanea, v.1900 (A).
  22. Chaniá:
    - a. Kanea, v.1900 (A);
    - b. Canea, 1906 (B);
    - c. Canea, 31.iii.1925 (S);
    - d. v.1968 (Wo).
  23. Katholikó:
    - a. grotte de Catholivo ou d'Agiou, 21.iv.1955 (Li) & cavité Catholivo ou Aghiou (B-S);
    - b. cavité Panagia (B-S);
    - c. Achyrosipilo, 21.iv.1955 (Li) & cavité Achyrosipilo (B-S);
    - d. Arkalo Spileo, Halbinsel Akrotiri, 200-300 m, v (? vi) 1926 (We); (precise location unknown).
  24. Moní Tzagaróliou: Kloster Aja Trias, Halbinsel Akrotiri, 26-28.ii.1925 (S).
  25. Akrotíri:
    - a. (C);
    - b. Akrotiri-Ebene, 30-70 m, v.1926 (We).
  26. Áptera:
    - a. Abdera, Eparchie Apokoronas, 9.x.1925 (S);
    - b. Ruinen und Gewölbe des Metellus Creticus, 200 m, v.1926 (We).
  27. Nísos Agíon Theodóron: ile D. Theodore (C).
  28. Eparchía Apokorónou (approximately):
    - a. plateau d'Apokorona (Luc);
    - b. Apocorona (C);
    - c. Apokorona, 9.x.1925 (S).
  29. Georgiούpolis: cavité (B-S).
  30. Alfíkampos: Ali Kampos, v.1900 (A).
  31. Askyfou, 750 m, 2.viii.1973 (Wi).
  32. Chóra Sfakíon: pentes de Sphakia (Luc).
  33. Komitádes, 18.iii.1925 (S).
  34. Kapsodásos, 19.iii.1925 (S).
  35. Frángo Kástello:
    - a. Frankokastelli, 25.v.1938, R. E. Gathorne-Hardy;
    - b. 5.v.1973 (Ga);
    - c. idem (O);
    - d. beach and dunes, 0-4 m, 3.viii.1973 (Wi).
  36. Skalotí, 19.iii.1925 (S).
- Nomós Réthminis:
37. Goniá:
    - a. environs de Gonia (Luc);
    - b. 23.iii.1904, D. M. A. Bate (location correct ?);
    - c. Megali Episkopi bis Gonia, 12.x.1925 (S).
  38. Réthimnon:
    - a. Rethymno, 21.v.1900 (A);
    - b. 13.x.1925 (S).
  39. Prasiés: Prasses, 23.x.1925 (S).
  40. Sélia, 450 m, 2.viii.1973 (Wi).
  41. Spíli, 600 m, 2.viii.1973 (Wi).

42. Patsós:
  - a. Patssos, 22.x.1925 (S);
  - b. Potami, nw. von Patssos, 22.x.1925 (S).
43. Loutrá: Lutra, 14.x.1925 (S).
44. Moní Arkádiou:
  - a. Kloster Arkadi, 16.x.1925 (S);
  - b. 8.v.1973 (O).
45. Moní Asomaton: Kloster Assomatos, 17.x.1925 (S).
46. Amári, 1906 (B).
47. Vizári:
  - a. Visari (C);
  - b. Visari, 24.v.1900 (A).
48. Áno Méros, 500-700 m, 1.viii.1973 (Wi).
49. Chordákion, 450 m, 1.viii.1973 (Wi).
50. Aghía Galíni:
  - a. 0-40 m, x.1972 (E);
  - b. 0-40 m, 31.vii.1973 (Wi).
51. Kouróutes: Kurutes, am Fuss des Psiloriti, 18.x.1925 (S).
52. Ídi Óros (approximately):
  - a. pentes d'Ida (Luc);
  - b. Mons Ida, 2200 m, 1906 (B).
53. Kolíta-Psilorítis, between hamlet Kolíta and summit Psilorítis (Ídi Óros), 1700-2100 m, 28-29.vii.1973 (Wi).
54. Nidha plateau:
  - a. Antrum Jovis, 1200-1500 m, 1906 (B);
  - b. Nidka-Hochebene und Andiskari, 11.v.1925 (S);
  - c. near the Idéon Ántron, 1370 m, 11.vi.1972 (K).
55. Anógia, 800 m, 10-15.vi.1972 (K).
56. Drosiá, 250 m, 23.x.1972 (E).

#### Nomós Irákliau:

57. Máraithos, 450 m, 26.x.1972 (E).
58. Spílios Camilari:
  - a. 5.iv.1955 (Li);
  - b. grotte annexe de Camilari, 2.iv.1955 (Li).
59. Krousónas: Krussona, 9.v.1925 (S).
60. Sárchos: grotte de Sarkhos, 10.iv.1955 (Li).
61. Síva, 300 m, 27.iii.1973 (Wi).
62. Asítes: Assitaes, M. Holtz.
63. Stavrákia, 300 m, 27.vii.1973 (Wi).
64. Tsagaráki, 15.x.1972 (E).
65. Aghía Varvára, 600-750 m, 21.x.1972 (E).
66. Megáli Vrísi: Megali Wryssi, 23.v.1925 (S).
67. Kamáres-Kolíta, along mountain track between village Kamáres and hamlet Kolíta (Ídi Óros), 520-1650 m, 28-29.vii.1973 (Wi).
68. Kamáres, 520 m, 28-29.vii.1973 (Wi).
69. Vorízia, 450 m, 27.vii.1973 (Wi).
70. Zarós: Saro, 15.v.1925 (S).
71. Phaistós:
  - a. near the excavations, 100 m, 23-26.v & 18.vi.1972 (K);
  - b. 1-2 km South of the ruins, wet meadows in the plain, 40 m, 24.v.1972 (K);
  - c. idem, 16 & 18.x.1972 (E);
  - d. idem, 30.vii.1973 (Wi).
72. Ághios Ioánis: Ajos Joannis, 16.v.1925 (S).
73. Míres: Myräs, 16.v.1925 (S).

74. Pitsíδια, dunes, 0-60 m, 30.vii.1973 (Wi).
75. Síva: Siwa, Ep. Pyrgiotissa, 7.v.1925 (S).
76. Moní Odigitrias: Kloster Hodigitria, Ep. Kānurion, 18.v.1925 (S).
77. Lásea, 18.v.1925 (S).
78. Moní Apezanón: Kloster Apeganās, Ep. Kānurion, 20.v.1925 (S) (correct ?).
79. Mesarás: plainē de Messara (Luc) (approximately).
80. Vourvoulitis: Wurwulitis, 22.v.1925 (S).
81. Loukia, 29.iv.1973 (Ga).
82. Archánes, 600-750 m, 19.x.1972 (E).
83. Knossós:
  - a. 29.v.1900 (A);
  - b. wayside, 17 & 21.v.1972 (K);
  - c. along brooklet, South of the ruins, 100 m, 10.viii.1973 (Wi).
84. Gázion, 7 km West of Iráklion, x.1972 (E).
85. Thérisos, also Lindo Beach or Lido, 3 km West of Iráklion, 0.3 m:
  - a. 19.v.1972 (K);
  - b. 14.x.1972 (E);
  - c. 25.ix.1973 (K).
86. Iráklion:
  - a. environs de Candie (Luc);
  - b. Kandia, 1900 (A);
  - c. Herakleion, 1906 (B);
  - d. 1-24.vi.1925 (S);
  - e. (Ge);
  - f. 5-12.iv.1975 (Lu).
87. Kornarouí, 6 km East of Iráklion, 10-15 m, 27.ix.1973 (K).
88. Neraídispilo ou grotte Ilithias, 4.iv.1955 (Li).
89. Florida Beach, 6 km East of Iráklion, 0-3 m, 26.ix.1973 (K).
90. Amnissós:
  - a. beach, 0-5 m, 20.v. & 16.vi.1972 (K);
  - b. 27.x.1972 (E);
  - c. 5-50 m, 29.ix.1973 (K).
91. Nísos Día: Insula Dhia, 1906 (B).
92. Skotinón:
  - a. Hagia Paraskevi à Scotino, 5.v.1955 (Li);
  - b. grotte Aghia Paraskevi, près du village de Skotino, ix.1971 (B-S).
93. Moní Agaráthou: Kloster Anagarathos, 27-28.v.1925 (S).
94. Xidás: Xyda, 27.vi.1925 (S).
95. Kastamonítsa, 27.vi.1925 (S).
96. Chersónisos: Chersonissos, 24.vii.1925 (S).
97. Mália:
  - a. inland of the ruins, 10-15 m, 18.v. & 9.vi.1972 (K);
  - b. 22-23. & 29.x.1972 (E);
  - c. along highway, 10 m, 9.viii.1973 (Wi);
  - d. beach, 0-5 m, 28.ix.1973 (K).
- Nomós Lassithíou:
  98. Vrachásion:
    - a. grotte Peristera, 11.v.1955 (Li);
    - b. idem (B-S).
  99. Mílatos:
    - a. grotte de Milatos, 12.v.1955 (Li);
    - b. idem (B-S);
    - c. grotte de Saint-Constantin, 12.v.1955 (Li).
100. Kato Metóchi, 28.vi.1925 (S).

101. Psichrón:
  - a. Psychro, 29.vi.1925 (S);
  - b. 850 m, 19.vi.1972 (K);
  - c. Psychro, 900 m, 7.viii.1939 (Ge).
102. Diktéon Ántron:
  - a. Dictéon antron, 7.v.1955 (Li);
  - b. grotte Diktaion Andron, ix.1971 (B-S).
103. Katharó plateau: Hochtal Catharo, 30.vi.1925 (S).
104. Kritsá, 330 m, 29.v.1972 (K).
105. Ághios Nikólaos:
  - a. St. Nikolo, v.1904 W.M.;
  - b. 0-5 m, 28-31.v.1972 (K);
  - c. 3 km North and South of the town, 0-50 m, 9.viii.1973 (Wi);
  - d. 31.iii.1975 (Lu).
106. Máles: Malás, 1.vii.1925 (S).
107. Anatolí:
  - a. Anadoli, 1.vii.1925 (S);
  - b. 400 m, 9.viii.1973 (Wi).
108. Graligiá, 0-5 m, 3.vi.1972 (K).
109. Xerókampos, 0-5 m, 2.vi.1972 (K).
110. Kalógeri: Kalogeros, 2.vii.1925 (S).
111. Ierápetra:
  - a. Jerapetra;
  - b. idem, 30.vi.1925 (S);
  - c. 0-5 m, 1.vi.1972 (K).
112. Káto Chorió: Kato Chorion, 3.vii.1925 (S).
113. Pachiámos, 4.vii.1925 (S).
114. Sfáka: Sphaka, 5.vii.1925 (S).
115. Tourtouli: Megali Katofyngui, 9.v.1955 (Li).
116. Sikiá, 400 m, 5.x.1973 (K).
117. Ághios Geórgios — Epáno Episkopí, 300 m, 5.x.1973 (K).
118. Chamézion: Chamesi, 6.vii.1925 (S).
119. Skopí, 100 m, 7.vi.1972 (K).
120. Piskokéfalon:
  - a. Piskocephalon, 7.vii.1925 (S);
  - b. 5 m, 7.x.1973 (K).
121. Pouáa Eklisiá: Russaklisia, 15.vii.1925 (S).
122. Sitía:
  - a. plateau de Sitia (Luc);
  - b. beach near the town, 0-3 m, 5.vi.1972 (K);
  - c. above the cemetery, 30 m, 6.vi.1972 (K);
  - d. hills West of the town, 50 m, 2.x.1973 (K);
  - e. wet meadows East of the Town, 2-3 m, 4.x.1973 (K);
  - f. v. Oertzen;
  - g. 2-16.v.1942, Wettstein.
123. Sitía, 5 km East of the town, beach, 0-5 m, 3.x.1973 (K).
124. Palékastron, 100 m, 3.x.1973 (K).
125. Vái:
  - a. mouth of the brook with *Juncus maritimus*, below zone of *Phoenix theophrasti*, 0 m, 3.x.1973 (K);
  - b. above the zone of *Phoenix*, 5 m, 3.x.1973 (K).
126. Ákra Síderos: Kap Sidero, 14.vii.1925 (S) (approximately).
127. Nísos Gianisáda: Insel Janisada.
128. Nísos Elása: Insel Elasa, 1887, v. Oertzen.

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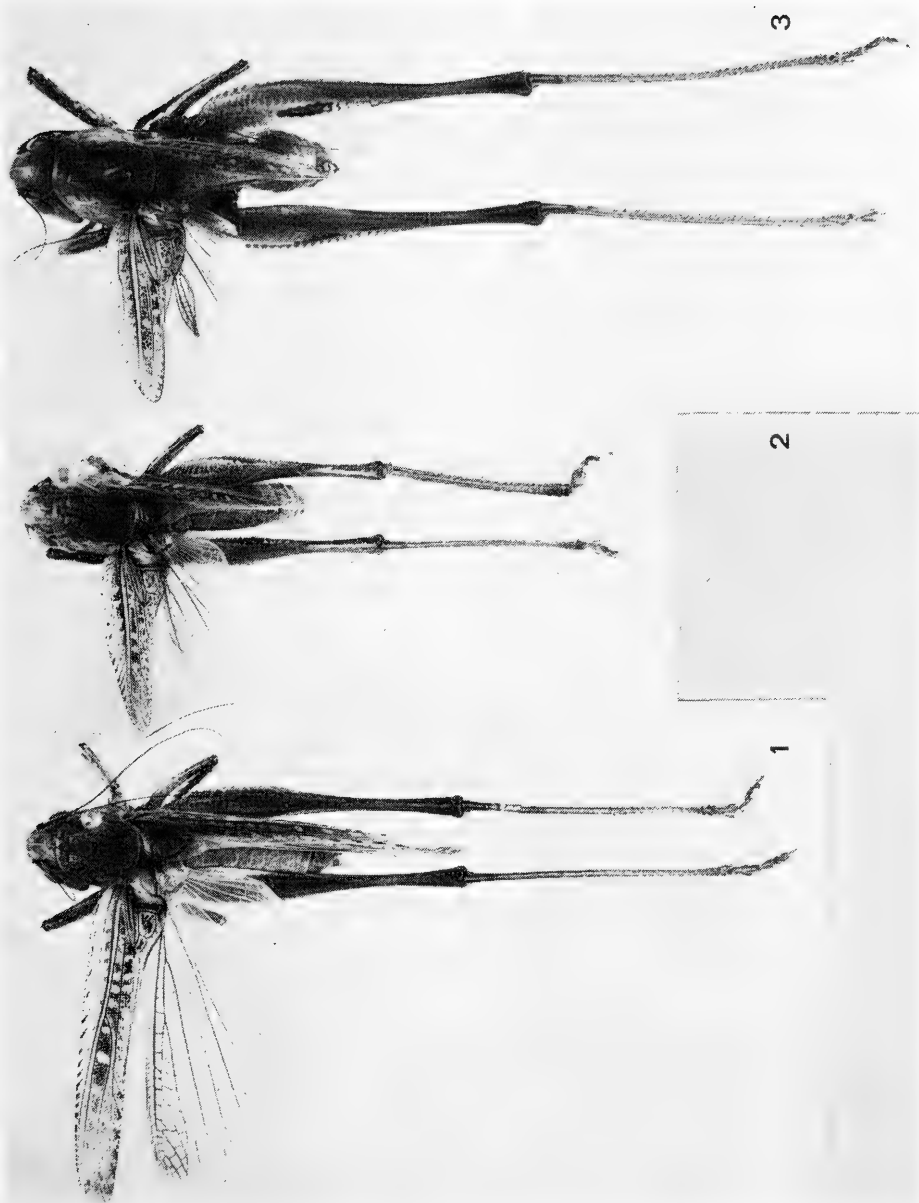
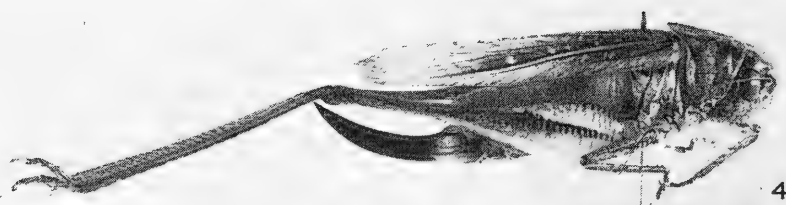


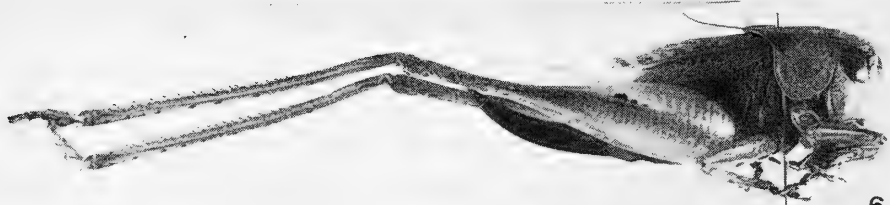
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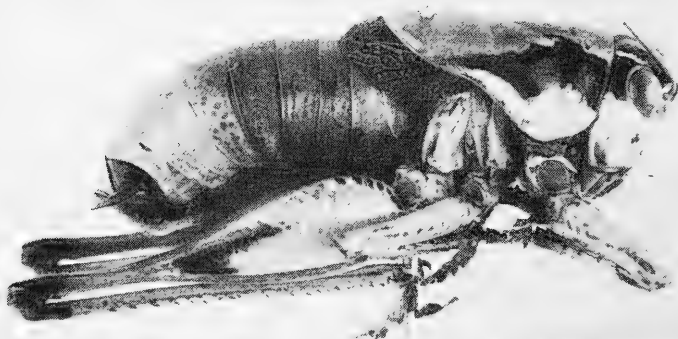
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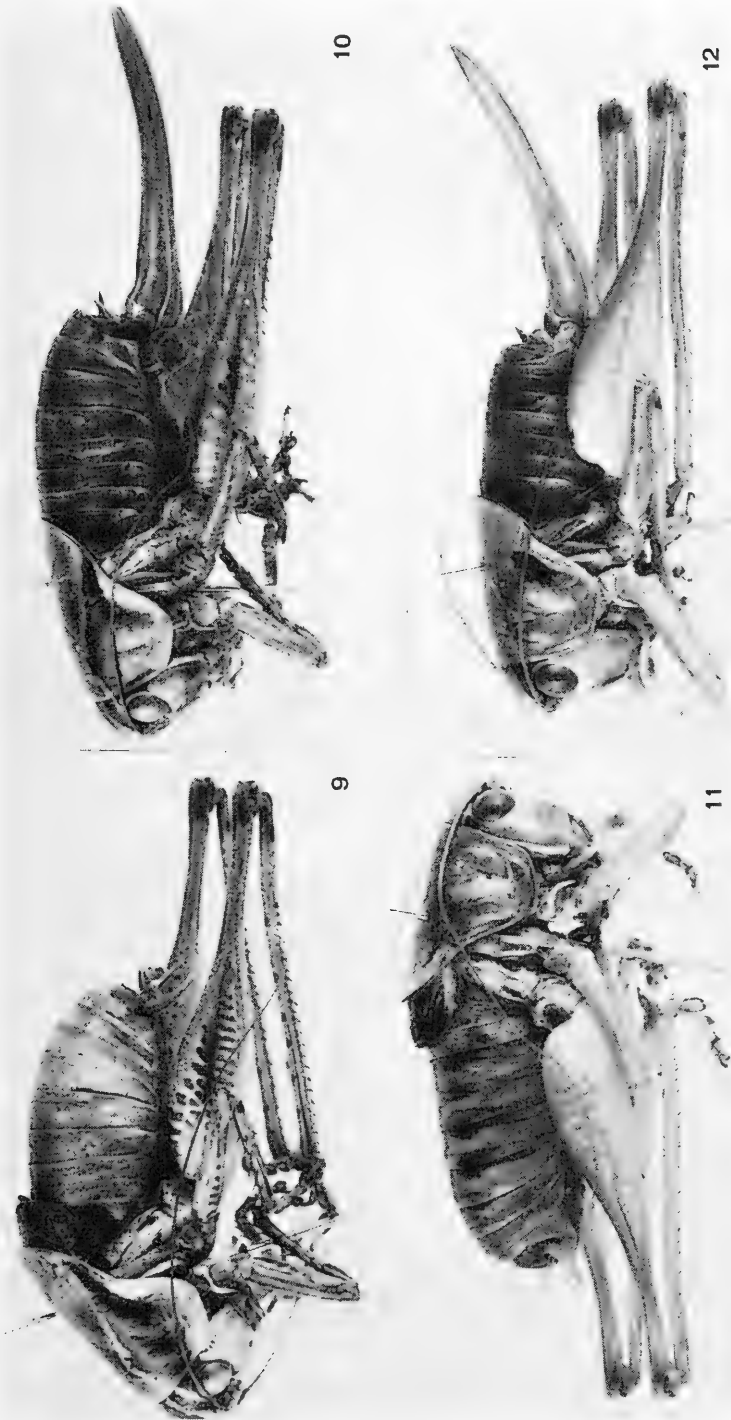


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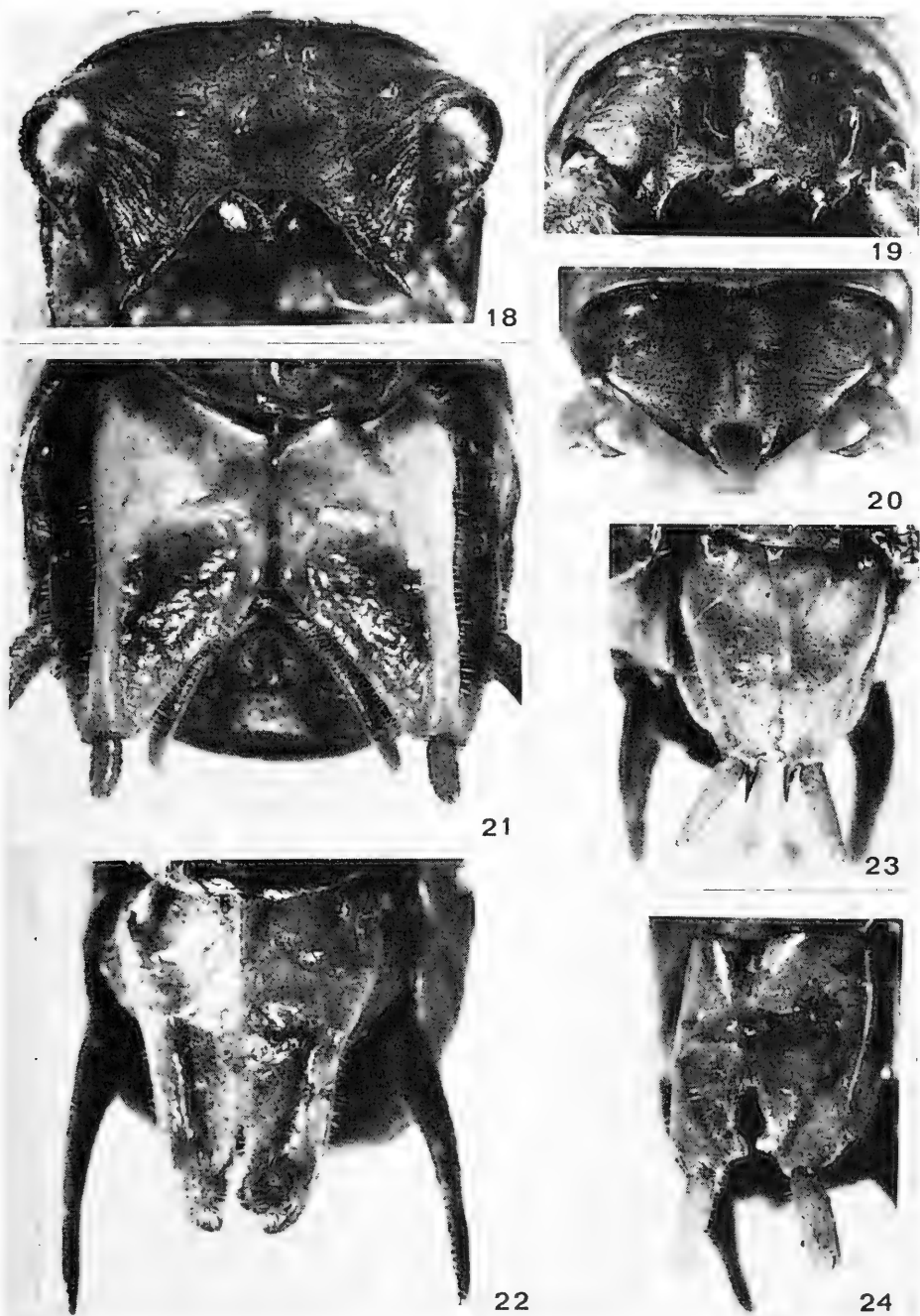


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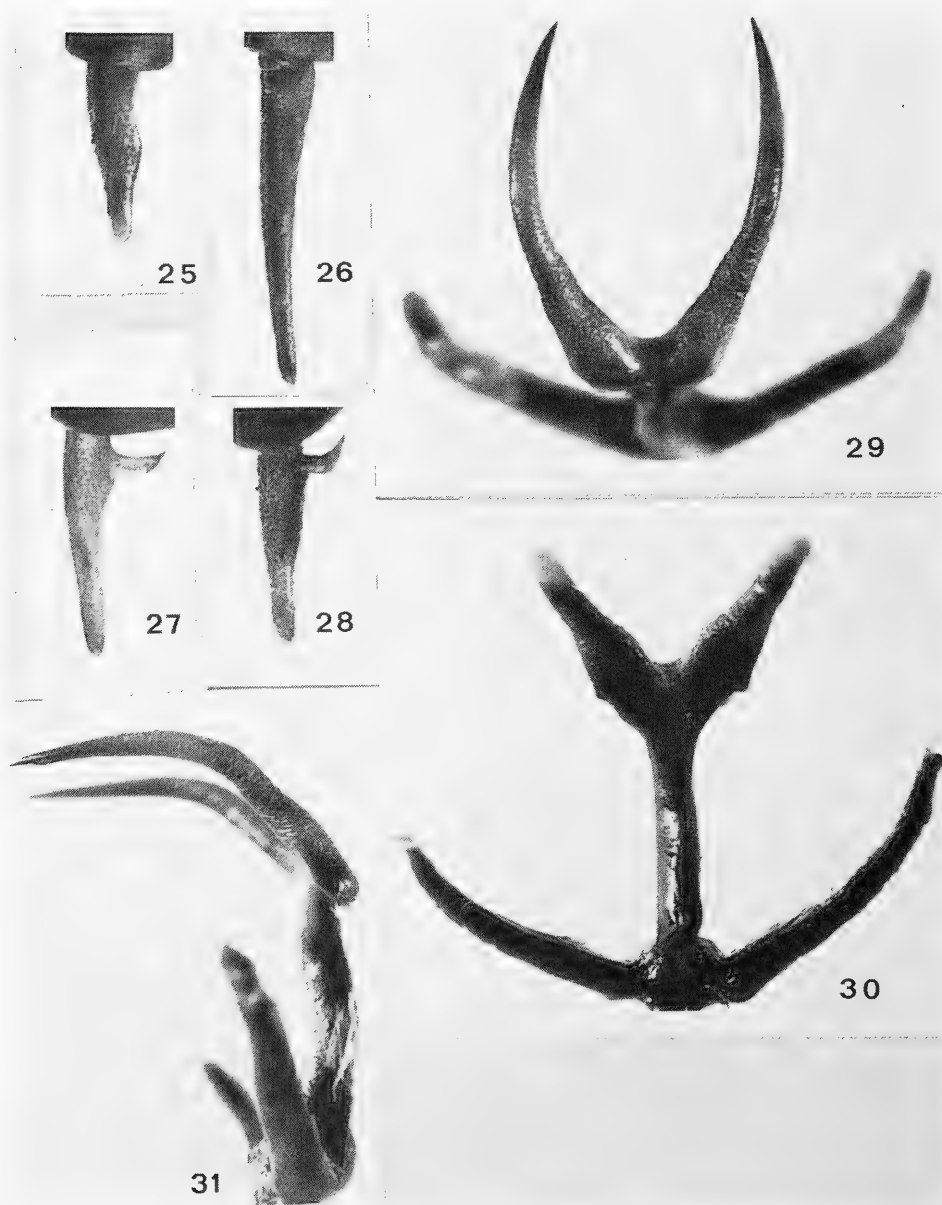


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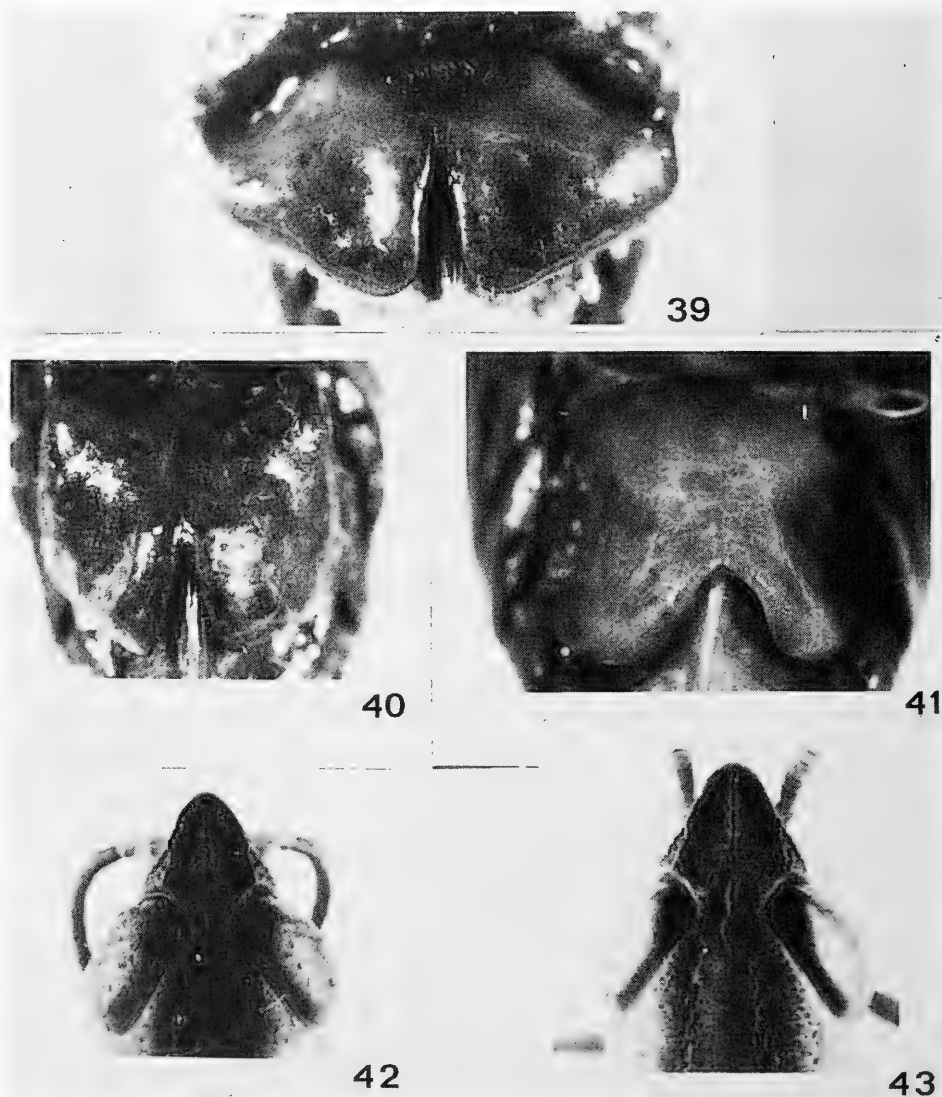


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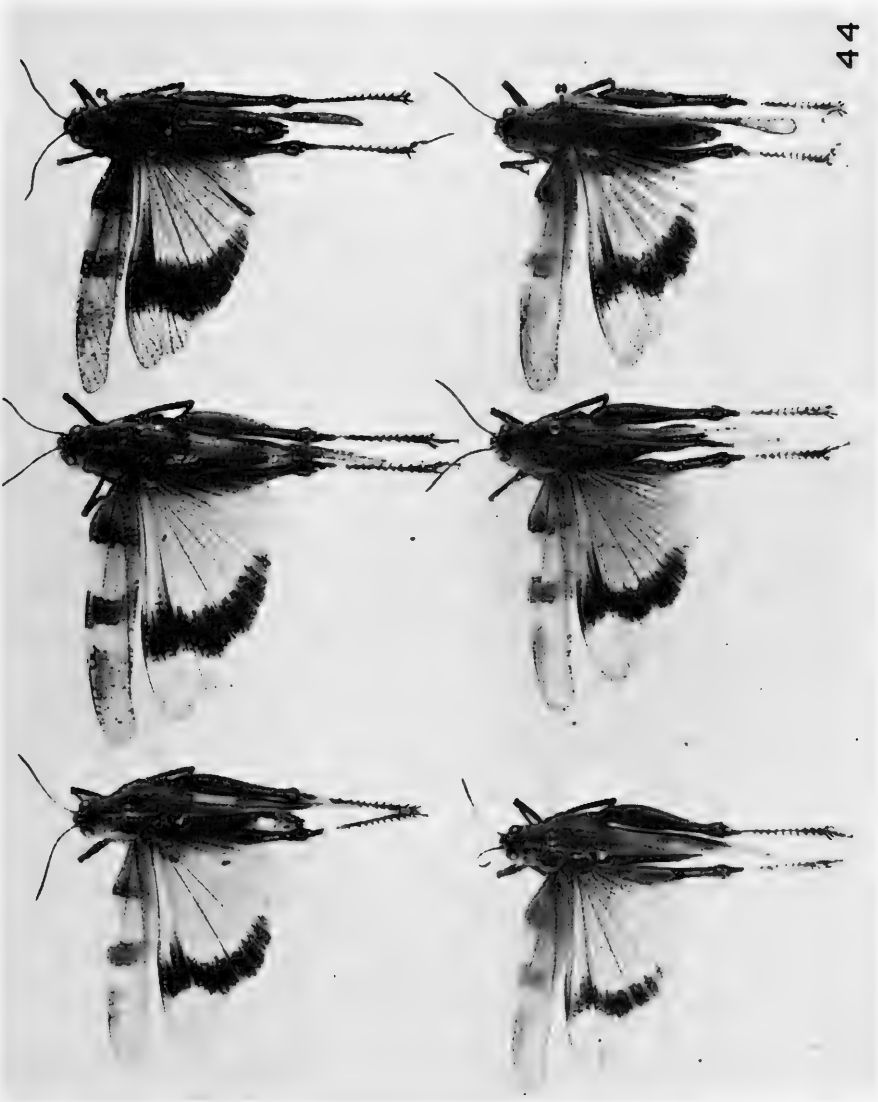


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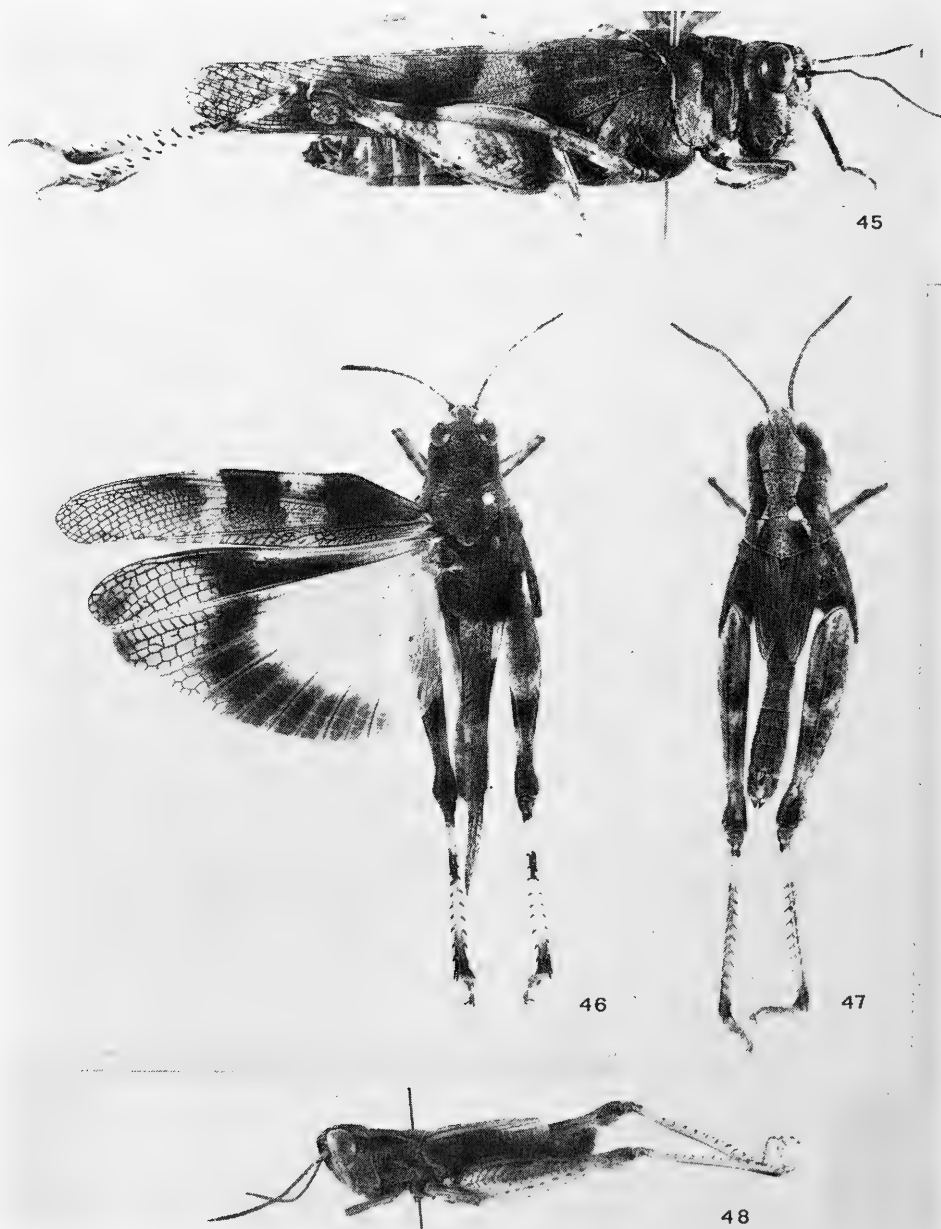


Fig. 45—46. *Oedipoda venusta* Fieber. 45, ♀, Anatolí (107b); 46, ♂, Linoséli (13). Fig. 47—48. *Chorthippus* (*Glyptobothrus*) *biroi* (Kuthy). 47, ♀, Linoséli (13); 48, ♂, Omalós (15e)







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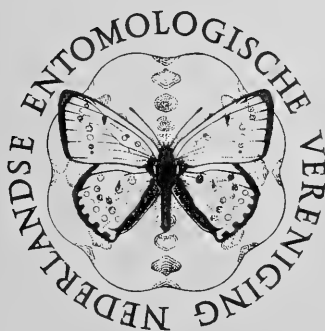
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## INHOUD

- R. DE JONG. — Affinities between the West Palaearctic and Ethiopian butterfly faunas, p. 165—215, fig. 1—10.



**AFFINITIES BETWEEN THE WEST PALAEARCTIC AND  
ETHIOPIAN BUTTERFLY FAUNAS**

by

**R. DE JONG**

*Rijksmuseum van Natuurlijke Historie, Leiden*

With ten figures

**ABSTRACT**

A survey is given of the species and genera common to the West Palaearctic and Ethiopian Regions. The possibilities of a faunal exchange in the past, especially during the Pleistocene, are analysed and related to the present distribution of West Palaearctic species in the Ethiopian Region and vice versa. It is demonstrated that faunal exchange across the Saharo-Arabian desert zone was not infrequently possible, but most invading species died out subsequently. Palaearctic species in the Ethiopian Region had a better chance to survive than Ethiopian species in the Palaearctic Region. Although the bare condition of the desert zone at present keeps the Palaearctic and Ethiopian Regions apart, it is concluded that the main factor inhibiting large-scale faunal exchange during the Pleistocene has been the repeated change of climate.

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## 1. INTRODUCTION

### General

This study is a zoogeographic one. It tries to describe the affinities between the butterfly faunas of the West Palaearctic and Ethiopian Regions and to explain these affinities with the aid of possible past distributions. As it deals with distributions, the ranges of the species have to be known and in this respect the butterflies form an attractive group, because possibly no insect group is better known.

This study also deals with history and, therefore, is concerned with evolution. In this respect, butterflies are probably scarcely better known than any other group of insects, as by far the greater part of the extensive literature on butterflies is faunistic (i.e., a description of the composition of species of a certain area) or a detailed analysis of the wealth of forms. At least the lower classification of the butterflies is still largely typological and evolutionary studies are almost absent. This is felt as a hindrance for the present paper, as an evolutionary study may reveal much of the probable geographic history (cf. De Jong, 1974). Nevertheless, there is no reason to suppose that an evolutionary study of the butterflies will necessitate many alterations in the classification and for the present paper I assume that the generally accepted genera are monophyletic. Further, if a genus has many representatives in region A, one of which occurs (possibly in another form) in region B, where it is the sole representative of the genus, it is concluded that this particular species invaded B from A. In some cases, viz. migrants, there is direct evidence of such invasions. In other cases, evidence or at least support should be looked for in an evolutionary study and in this way the present paper may serve to indicate some of the many gaps in our knowledge.

I have attempted to give the total number of species known for each genus, but have often failed to find agreement in literature. This is due partly to (sometimes excessive) splitting of genera and species, partly to the fact that, usually, regional faunas instead of whole genera have been studied and I cannot help thinking that various degrees of "intuition" have played a part. It is, for instance, difficult to estimate the number of species in the genus *Lycaena* (the Coppers). Kostrowicki (1969) lists 30 species in the Palaearctic Region, but generally this genus is divided into four genera (*Heodes*, *Lycaena*, *Thersamonia* and *Palaeochrysophanus*) in the West Palaearctic. For Central Europe, Forster & Wohlfahrt (1955) place the species *helle* and *phlaeas* in *Lycaena* s.s. and *dispar* in *Thersamonia*, while Higgins & Riley (1970) consider *dispar* congeneric with *phlaeas*. If there is so much disagreement in the best known part of the world, how about the Asiatic species, for which Verity (1943) introduced two more genera. In such cases it seems most practical to record the number of species in the collective genus, in the above case

*Lycaena* s.l. In the text it is specified how the total number of species in a genus has been arrived at. It is not of crucial importance for the present study. So far as the genera can be considered monophyletic, large genera may be preferable for the present kind of study, as they may give a good impression of the relative development of a group of species in various regions, e.g. the very strong development of the Coppers (*Lycaena* s.l.) in the Holarctic Region as opposed to the very poor representation outside this area. On the other side, however, it is also indicative to observe that the Coppers in the Holarctic Region can be divided into six genera, while only one of these genera, with a single group of species, occurs in the Ethiopian Region. An advantage of the use of many small genera is that it is easier for a non-specialist to trace closely related species (if the small genera are considered monophyletic, what can only be assumed as they are usually based typologically).

The affinities between the West Palaearctic and Ethiopian butterfly faunas have been studied up to the generic level, i.e. only common genera have been considered. The affinities based on related instead of common genera have been regarded too remote to be studied successfully on the basis of the present-day knowledge of both the phylogeny of the butterflies and the geographic and climatic changes in the more remote past. Another limitation to the present paper is the area studied. As is known many Oriental genera penetrate the Palaearctic Region in East Asia. Some of these genera (e.g. *Graphium*, *Appias*, *Mycalesis*, *Deudorix*) also occur in the Ethiopian Region and in such cases it is probable that the affinities between the Palaearctic and Ethiopian Regions are indirect, via the Oriental Region. To exclude such cases, only the butterfly genera occurring in the West Palaearctic Region, west of about 50° E Long. (thus including Europe and the Middle East), have been considered.

### The Palaearctic-Ethiopian boundary

There is some disagreement about the boundary between the Palaearctic and Ethiopian Regions. Darlington (1957), for instance, delimited the Ethiopian Region as the whole of Africa except the parts of Morocco and Algeria north of the Atlas Mountains, while De Lattin (1967) sets the boundary along the southern edge of the Sahara. There is no reason to enter here into a discussion on the use of distinguishing zoogeographic regions, but as descriptive, geographic terms they have at least practical value, provided they are clearly defined. The obstacle in defining the boundary between the Palaearctic and Ethiopian Regions is the position of the Sahara. Although often the peculiar character of its fauna is recognized, the Sahara is still usually considered a transition zone. Geographically the Sahara is, indeed, the transition between the tropical parts of Africa and the warm-temperate parts of the northern part of the Old World. Ecologically, however, speaking in terms of major habitats, the Sahara is a life zone, a biome, comparable in this respect to, e.g., the taiga or the sea. I never saw the taiga considered the transition between the deciduous forests to the south and the subarctic birch forest to the north. And there is apparently little meaning in calling the sea the transition zone between two land masses or in regarding Africa the

transition zone between the Atlantic and Indian Oceans, just because it lies in between.

The zoogeographic distinction of the Palaearctic and Ethiopian Regions is based on a different faunal composition. This difference can, at least partly, be explained as the result of a separated faunal development, i.e. there has been a barrier preventing free faunal exchange. Evidently the main barrier has been and is the Sahara.

These considerations lead to the assumption that the boundary between the Palaearctic and Ethiopian Regions does not run north or south of or straight across the Sahara, but is the Sahara itself. Studying the affinities between the butterfly faunas of the Palaearctic and Ethiopian Regions is studying the function of the Sahara as a barrier, at present and in the past. As a consequence, only those genera and species are considered common to both regions, which occur north as well as south of the Sahara.

The area studied has been extended to the east to cover the Arabian peninsula, extending the barrier to the Saharo-Arabian desert zone and regarding Yemen the north-eastern outpost of the Ethiopian Region.

## 2. RANGE, ECOLOGY AND RELATIONSHIP OF GENERA AND SPECIES OF BUTTERFLIES COMMON TO THE WEST PALAEARCTIC AND ETHIOPIAN REGIONS

*Papilio*. A cosmopolitan genus with a large development in the tropics, but with only three species in the West Palaearctic, viz. *machaon* L., *hospiton* G  n  , and *alexanor* Esper. The Ethiopian fauna comprises about 50 species. Over the whole more than 200 species are known. The West Palaearctic species are placed by Munroe (1960) in the *machaon* group, which ranges throughout the Holarctic Region and into Central America. Together with the East Palaearctic *xuthus* L., they are thought to be closely related to the *demoleus* group, which occurs in the Ethiopian and Oriental Regions and extends eastward to Papua.

*Pieris*. Much disagreement exists in the delimitation of the genera *Pieris* and *Pontia*. Part of the disagreement is shown in Table 1. The number of species allocated to *Pieris* varies from about 18 to about 26, see e.g. Talbot (1932a) and Bernardi (1947). Of these six to nine are confined to the New World. In the Old World the genus is almost strictly Palaearctic, but some species extend far into the Oriental Region (*canidia* Sparrman, *melete* M  n  tri  s) or occur near the edge of the Palaearctic (*naganum* Moore). One species, *rapae* L., has been imported as far as New Zealand (Laidlaw, 1970). Apparently, an Oriental development of the genus is absent. In the Ethiopian Region there is a single, endemic species, viz. *brassicoides* Gu  rin, which is restricted to the montane grasslands of Ethiopia and N. Tanzania (Carcasson, 1964). The latter population was distinguished as ssp. *meridionalis* Joicey et Talbot. According to Lagnel (1966) *brassicoides* can be considered to form a superspecies together with *brassicae* L. (Canary Islands, N. Africa and W. Europe to Yunnan) and *deota* De Nic  ville (Issyk-Kul to Ladak). The common European *brassicae* (Large White) can be found everywhere in flowery places from lowlands up to 2000 m (Fig. 3).

*Pontia*. Part of the disagreement on the delimitation of this genus is shown in



Table 1. We are here mainly interested in the first four species on which there is no disagreement with regard to the genus they belong to and which as a group occur in the Ethiopian and Palaearctic Regions. But to place their evolution in a wider perspective, also the other, probably closely related species listed in Table 1

Table 1. Allocation of species to *Pontia* and related genera by various authors

	Talbot (1932a)	Verity (1947)	Bernardi (1947)	Dos Passos (1964)	Higgins & Riley (1970)
<i>daplidice</i>	<i>Pontia</i>	<i>Pontia</i>	<i>Pontia</i>	—	<i>Pontia</i>
<i>glaunome</i>	<i>Pontia</i>	<i>Pontia</i>	<i>Pontia</i>	—	—
<i>distorta</i>	<i>Pontia</i>	<i>Pontia</i>	—	—	—
<i>helice</i>	<i>Pontia</i>	<i>Pontia</i>	—	—	—
<i>chloridice</i>	<i>Pontieuchloia</i>	<i>Pontieuchloia</i>	<i>Pieris</i>	—	<i>Pontia</i>
<i>beckeri</i>	<i>Pontieuchloia</i>	<i>Pontieuchloia</i>	<i>Pieris</i>	<i>Pieris</i>	<i>Pontia</i>
<i>protodice</i>	<i>Pontieuchloia</i>	<i>Synchloe</i>	<i>Pieris</i>	<i>Pieris</i>	—
<i>sisymbrii</i>	<i>Pontieuchloia</i>	<i>Synchloe</i>	<i>Pieris</i>	<i>Pieris</i>	—
<i>callidice</i>	<i>Synchloe</i>	<i>Synchloe</i>	<i>Pieris</i>	—	<i>Pontia</i>
<i>dubernardi</i>	<i>Synchloe</i>	<i>Synchloe</i>	<i>Pieris</i>	—	—
<i>davidis</i>	<i>Synchloe</i>	<i>Synchloe</i>	<i>Pieris</i>	—	—
<i>nigricans</i>	<i>Synchloe</i>	<i>Synchloe</i>	<i>Pieris</i>	—	—

have to be considered and without choosing for one of the classifications mentioned the following observations may be important for the present study:

a. All species of Table 1 are confined to some part of the Holarctic Region, except the first four species, two of which are Ethiopian, while the other two occur in both the Ethiopian and Palaearctic Regions.

b. *Pontieuchloia* is considered intermediate between *Pontia* and the almost exclusively Holarctic *Euchloe* (Verity, 1947).

c. According to Verity (1947) the last three species of Table 1 are intermediate between *Synchloe* and the Palaearctic genus *Aporia*.

All these observations point to an almost entirely Holarctic group of species with a slight development in the Ethiopian Region. As related genera occur in the Palaearctic and not in the Ethiopian Region, the Palaearctic origin of the Ethiopian members seems obvious.

The ranges, etc., of the first four species of Table 1 are as follows:

*daplidice* L. — From France to Japan (Higgins & Riley, 1970); Canary Islands (Van Regteren Altena, 1949); N. Africa south to Tibesti (Bernardi, 1962). In all these regions there is little geographic variation (though various subspecies have been described), possibly due to the fact that the species, at least in Europe, is strongly migratory. A separate subspecies (*aethiops* Joannis et Verity) is recorded from Ethiopia, Somalia and Yemen (Gabriel, 1954). *P. daplidice* prefers rough grounds and flowery meadows.

*glaunome* Klug. — An eremic species occurring from Mauretania to Ethiopia, Kenya, Somalia and Sinai and through Arabia and Mesopotamia to NW. India. The African and Arabian populations are thought to be subspecifically distinct (ssp. *glaunome* Klug) from the more eastern populations (ssp. *iranica* Bien.).

*distorta* Butler. — Restricted to Somalia and Kenya (Aurivillius, 1910—25). Probably also a more or less eremic species.

*helice* L. — A common species throughout S. Africa (Swanepoel, 1953), north to

S. Botswana and S. Rhodesia (Van Son, 1949). Further, in the montane grasslands of E. Africa (Kivu, Tanzania, Uganda, Kenya) as a separate subspecies (*johnstoni* Crowley) (Fig. 5).

*Euchloe*. This genus is divided by Bernardi (1945) and Verity (1947) into two subgenera, viz. *Elphinstonia* and *Euchloe*. Higgins & Riley (1970) consider *Elphinstonia* a separate genus, but their allocation of species to *Euchloe* and *Elphinstonia* is different from Bernardi's and Verity's. This difference of opinion is unimportant for the present study and we will distinguish a single genus, like Bernardi did, but without bothering about subgenera.

The genus *Euchloe* comprises ten species. Three species are confined to N. America; the remainder are Palaearctic, but two species also occur in the Ethiopian Region, viz.:

*belemia* Esper. — SW. Europe, Canary Islands, N. Africa (also Tibesti) to Iran and Baluchistan (Higgins & Riley, 1970). In the Ethiopian Region it is known from Ethiopia and Somalia (Talbot, 1932b; Carpenter, 1935). The Ethiopian populations are distinguished as ssp. *abyssinica* Riley. This species prefers rough, flowery places, usually at low levels. It is a strong flyer; in S. Spain I had no difficulty in distinguishing this species among other spring species like *Pontia daplidice*, *Euchloe ausonia* and *Pieris rapae*, by its flight only.

*falloui* Allard. — More eremic than *belemia*, ranging far into desert oases and occurring throughout N. Africa, including Tibesti, Fezzan, Tripoli, and Egypt, but in the north-west mainly south of the Atlas Mountains (Higgins & Riley, 1970). In the Ethiopian Region it has been found in Somalia. According to Talbot (1932a) the Somalia population represents the same subspecies as which flies in S. Algeria (*obsolescens* Rothschild). Gabriel (1954) recorded this species from SW. Arabia, with the comment that this population may represent a separate subspecies.

*Colotis*. An Indo-African genus, with 40 Ethiopian species (Carcasson, 1964) and seven species in India and Ceylon (Wynter-Blyth, 1957). Almost all species occur in open and usually dry country and many species live partly or exclusively in semidesert environments. There are no endemic Palaearctic species, but some species penetrate into the southern parts of the Palaearctic. They are:

*evagore* Klug. — Throughout the Ethiopian Region (Williams, 1969) and in Yemen (Gabriel, 1954); as a separate subspecies, *nouna* Lucas, in Morocco, Algeria, Tunis and S. Spain (Higgins & Riley, 1970) (Fig. 7).

*fausta* Oliv. — India to Egypt and SW. Arabia; north to Israel and Jordania (Hemming, 1932) and, as a migrant, in Lebanon and sometimes Turkey (Larsen, 1974). Although it is a common species in Lebanon, *fausta* appears unable to hibernate there.

*calais* Cramer. — Through most of the Ethiopian Region outside forest areas. In the Oriental Region in India and Ceylon. It occurs in Yemen (Gabriel, 1954) and seems to be resident as far north as Ennedi (Bernardi, 1964) and the Air Mountains (Rothschild, 1921) in the Sahara, and the Jordan Valley (Larsen, 1974). Talbot (1934) considered the E. Mediterranean form indistinct from the Indian one, but according to Gabriel (1954) and Larsen (1974) the African form flies there.

*phisadia* Godart. — NW. India, Arabia to Nubia, Ethiopia, Somalia, Kenya, Senegal (Talbot, 1934) and Rio de Oro (Bernardi, 1966). Also known from Ennedi, Tibesti, Ahaggar and Aïr (cf. Table 5) in the Sahara. Talbot mentioned Madagascar but this seems an improbable locality. In Israel and Jordania it flies as *ssp. palaestinensis* Staudinger (Hemming, 1932; Talbot, 1934).

*chrysonome* Klug. — According to Talbot (1934) from S. Israel and Jordania through Arabia, Nubia and Somalia to Tanzania and N. Rhodesia; further in N. Nigeria and Rio de Oro (Bernardi, 1966) and mentioned from Ennedi, Tibesti, Ahaggar and Aïr in the Sahara (cf. Table 5).

*Anaphaeis*. A palaeotropical genus with two species in the Indo-Australian Region and seven in Africa and Madagascar. There are no endemic Palaearctic species. The species *aurota* Fabr. occurs throughout Africa south of the Sahara, in a variety of habitats, from forest edges to semidesert bush (Williams, 1969). Further north it occurs in Sudan, Egypt and Arabia (Gabriel, 1954) and, as a migrant, in Lebanon (Larsen, 1974) and Jordania (Hemming, 1932). It extends further east through India to Ceylon (Wynter-Blyth, 1957).

*Catopsilia*. This genus has a peculiar distribution. According to Talbot (1932a) there are three species in Madagascar (and Mauritius) and five in the Indo-Australian Region, while one species, viz. *florella* Fabr., flies throughout the Ethiopian Region and extends via Egypt and Arabia to India, China and Hainan. Only since 1966 it is known from the Canary Islands where it has become established probably as a result of migration (Manley & Allcard, 1970). It has been found as a migrant in Lebanon (Larsen, 1974) and Iraq (Wiltshire, 1957).

*Colias*. This genus reaches its greatest development in the Holarctic Region where about 50 species occur (36 in the Palaearctic). In the Neotropical Region 12 species are known. Although 14 species have been found in India, they cannot be regarded Oriental residents, as they are confined to the higher altitudes of the Himalayas, with the exception of *erate* Esper (Wynter-Blyth, 1957). The literature is somewhat confused about the identity of the Indian *erate*, but that is not important here. The Indian *erate* occurs in NW. India (Chitral to Kumaon) and in the S. Indian mountains.

In the Ethiopian Region two species of *Colias* are known, viz.:

*erate* Esper. — Palaearctic, from E. Europe to Japan and Formosa (Higgins & Riley, 1970) and in India (see above). Further in Ethiopia, Somalia, Sudan, Egypt and SW. Arabia (Gabriel, 1954) (*ssp. marnoana* Rogenhofer).

*electo* L. — According to Williams (1969) distributed over the greater part of Africa south of the Sahara, in grasslands, along forest edges, etc., but I have not found data on its occurrence in W. Africa. Outside Africa, it has been found in Yemen en Saudi-Arabia (Gabriel, 1954). Aurivillius (1910.—25) and Van Son (1949) regarded *electo* conspecific with *crocea* Geoffroy, but various authors (e.g. Lempke, 1944 (1946); Jarvis, 1953) concluded on typological grounds that *crocea* and *electo* are specifically distinct. *C. crocea* is a well-known migrant in Europe which occurs from the Azores, Madeira and Canary Islands through N. Africa and S. and C. Europe to Iran (Higgins & Riley, 1970). In N. Africa *crocea* goes as far south as Tibesti (Bernardi, 1962).

Jarvis (1953) suggested that the E. African form of *electo*, *pseudohecate* Berger, could be a species separate of *electo*, but we will not busy ourselves with such speculations.

Note. I have no special knowledge of the genus *Colias*, but it appears to me that the Ethiopian species can be considered to belong to two species groups, viz.:

a. the *hyale* group, comprising *hyale* L. (C. Europe to Altai; strongly migratory), *australis* Verity (S. and C. Europe to S. Russia and Turkey; possibly migratory) and *erate* Esper (E. Europe to Japan and Formosa; south to Ethiopia, Somalia, S. India).

b. the *crocea* group, comprising *crocea* Geoffroy (W. Palaearctic to Iran; strongly migratory), *fieldii* Ménétériés (N. India to N. Burma, at higher altitudes) and *electo* (Ethiopian Region to Arabia) (cf. Lempke, 1944 (1946); Jarvis, 1953).

Classified in this way it is striking that these groups are the only groups of *Colias* species in the Old World represented outside the Palaearctic Region, and that both possess at least one species that is strongly migratory. It seems inevitable to consider the Ethiopian species Palaearctic invaders.

*Danaus*. A pantropical genus with about 60 species. A few species occur in the Nearctic Region, a few others penetrate the Palaearctic Region in the east and two have been found in the W. Palaearctic, mainly as migrants. They are:

*plexippus* L. — An American species that since 1880 is resident in the Canary Islands. It also occurs in the Azores. Rare vagrants reach Portugal, Spain, France, Ireland and England (Higgins & Riley, 1970). This species has extended its range from America particularly in western direction, largely aided by man, and it now occurs in Hawaii, New Zealand, Australia, Papua, Indonesia, Formosa and the Andaman Islands (Klots, 1951; Higgins & Riley, 1970). It is absent from Africa and continental Asia.

*chrysippus* L. — A very common species throughout the Ethiopian Region, in open and bush country, gardens, woodlands, margins of forests (Williams, 1969). Resident in the Canary Islands. North to Lebanon and thence eastward throughout tropical Asia to Australia; vagrants occasionally found in Morocco, S. Italy and Greece (Larsen, 1974). In Africa it occurs in two subspecies:

a. ssp. *alcippus* Cramer. — W. Africa south of the Sahara, north to S. Morocco and also found in Aïr, Tibesti and Ennedi in the Sahara.

b. ssp. *chrysippus* L. — Whole of Africa, except the west; eastern Mediterranean and thence eastward. According to Bernardi (1962) this form also occurs in the Canary Islands, but Manley & Allcard (1970) list the form of that area as a distinct, endemic subspecies (*kanariensis* Fruhst.).

*Libythea*. A peculiar, cosmopolitan genus with about ten species (the two New World species are classified by Dos Passos, 1964, in a separate genus). Pagenstecher (1901) distinguished two subgenera in the Old World, viz. *Libythea* with six species, in Europe, Asia and Australia; and *Dichora* with three species, in the Ethiopian Region (one confined to Madagascar and Mauritius). Williams (1969) considered one of the Ethiopian species of Pagenstecher (*laius* Trimen) a subspecies of the Ethiopian *labdaca* Westwood, and according to Corbet & Pendlebury (1956) *labdaca* is the Ethiopian representative of the Oriental *narina*

Godart, so that the distinction of two subgenera is insignificant.

In the West Palaearctic only *celtis* Laich. occurs. Its range extends from S. Europe and N. Africa to Japan and Formosa. From the above it seems improbable that there is a direct relationship between the West Palaearctic and Ethiopian species.

*Charaxes*. A palaeotropical genus with 86 species in Africa south of the Sahara (Carcasson, 1964) and more than 20 in the Indo-Australian Region. There is only a single species occurring in the Palaearctic Region and this species also flies throughout the Ethiopian Region, viz. *jasius* L. (Fig. 9). It was apparently by mistake that Carcasson called *Charaxes* a Palaearctic genus.

The distribution of *jasius* in the Palaearctic is confined to the coastal areas around the Mediterranean. South of the Sahara, *jasius* occurs in two distinct geographic forms all over the continent, in savanna country, woodlands and bush.

*Neptis*. Apart from a large development in the Ethiopian Region (47 species; Carcasson, 1964), there are many species confined to the Indo-Australian area (31) and to the Palaearctic (18), while 20 species occur in both the Palaearctic and Oriental Regions (Eliot, 1969). Most Palaearctic species are confined to East Asia, often to the contact zone with the Oriental Region; only two species occur as far west as Europe:

*sappho* Pallas. — A woodland species, distributed from C. Europe (Salzburg) to the Amur region, Japan, Formosa and S. Vietnam, in a number of subspecies.

*rivularis* Scopoli. — Also a woodland species, from the Southern Alps (Piedmont) to Kamchatka, Kurile Is., Japan, Formosa and Szechwan, in a number of subspecies.

There is no apparent reason to suppose a close relationship between the two mentioned species and the Ethiopian members of the genus. On the contrary, the European species appear Asiatic invaders in Europe, judged from their present distribution.

*Hypolimnas*. A palaeotropical genus with a twenty odd species. Two species occur in Africa as well as in the Indo-Australian area and one of these, *misippus* L., is rarely found as a migrant in Lebanon, probably coming from Egypt, where it is common (Larsen, 1974). This species has a very extensive range. It occurs from Madagascar and Africa (where it is common everywhere in open country, bush, etc.; Williams, 1969) to India, SE. Asia, New Guinea, Solomons Islands, and Australia. It was supposedly introduced into the Antilles from Africa in slave ships some centuries ago and has been found not only in the West Indies, but also north into the USA and in northern S. America (Common & Waterhouse, 1972).

*Vanessa*. This genus was recently dealt with by Field (1971), who thought it necessary to split *Vanessa* in three genera, viz. *Vanessa*, *Bassaris* and *Cynthia*. In my opinion this splitting is somewhat superfluous, as for the reflection of the affinities within the genus the distinction of species groups or subgenera would have done and nomenclatorial troubles would have been avoided. I deal with the genera of Field here as subdivisions of the genus *Vanessa* s.l. This genus is, with 16 species, distributed all over the world. Four species have been found in the West

Palaeartic and one of these is the sole representative of the genus in the Ethiopian Region. They are:

*atalanta* L. — According to Field (1971), a Holarctic species that is introduced in Hawaii, but Higgins & Riley (1970) thought its Palaeartic range not to extend eastward beyond Iran. No subspeciation within the Palaeartic. It is a well-known migrant in Europe and in the northern part of its range it reintroduces itself each year by migrations from the south.

Together with the following and three other species, *atalanta* belongs to *Vanessa* s.s., which is distributed in the Holarctic and Oriental Regions.

*indica* Herbst. — This species shows a peculiar distribution: it is widely distributed in India, China, Korea and Japan, and quite separated from this range it occurs in Madeira and the Canary Islands (distinguished as ssp. *vulcanica* Godart).

*cardui* L. — The most cosmopolitan butterfly, found everywhere, except in Australia and New Zealand (where it is replaced by *kershawi* M'Coy) and in arctic and antarctic regions. It is rare in S. America south of Venezuela. This species is strongly migratory and this may be the reason why there is no geographic variation, though subspecies have been described (see Field, 1971). In much of Europe, *cardui* cannot hibernate, but can produce a summer generation. It is the only *Vanessa* species in Africa. With the Australian *kershawi* and seven New World species *cardui* forms what Field called the genus *Cynthia*.

*virginiensis* Drury. — One of the New World species of Field's *Cynthia*, occurring from Canada to Colombia and Venezuela and possibly much further south (Field, 1971). Field recorded this species to have become established by migration in Hawaii, the Azores, Madeira and the Canary Islands, but Higgins & Riley (1970) and Manley & Allcard (1970) only mentioned the Canary Islands, as far as the Palaeartic is concerned. Since 1948 many specimens have been found in Portugal and some also in Spain, as far as the Pyrenees (Gomez Bustillo & Rubio, 1974). No subspecies are known.

*Precis*. In the Old World this genus is almost entirely confined to the tropics, but in the New World it extends over North and South America. From the Ethiopian Region 29 species are known, from the Indo-Australian Region 11, some of which have a palaeotropical distribution. Only two species have been found, at least one as a migrant, in the Palaeartic region, viz.:

*hierta* Fabr. — An abundant species throughout the Ethiopian Region in open country (Williams, 1969); Arabia (Gabriel, 1954); eastward through India (where it is very common; Wynter-Blyth, 1957) to Ceylon and Hongkong (Fruhstorfer, 1912). In the Palaeartic it has only been found in the Lebanon, some 60 years ago. Larsen (1974) thinks that it may have been imported, rather than having made its own way to the Lebanon.

*orithya* L. — Another palaeotropical species, abundant in open, dry country throughout the Ethiopian Region (Williams, 1969) and extending eastward through Arabia and India to Australia (Gabriel, 1954). It is an immigrant in Iraq, where it prefers oases and river banks (Wiltshire, 1957), but I have not found indications about the origin of the Iraqi immigrants.

*Issoria*. As delimited by Warren (1956) this genus comprises three species groups, a Palaearctic, an Ethiopian, and a S. American one. Only one of the three Palaearctic species occurs in the W. Palaearctic, viz. *lathonia* L. (Canary Islands, N. Africa and W. Europe to Szechwan and through the Himalayas to Bhutan; Higgins & Riley, 1970; Fruhstorfer, 1912); the other two Palaearctic species are confined to Asiatic mountains.

The Ethiopian species group is composed of three species, viz. *hanningtoni* Elwes, *smaragdifer* Butler, and *excelsior* Butler, distributed over the mountains of E. Africa, south to Malawi, and the Cameroon highlands.

The S. American group numbers five species and is mainly confined to Chili (southward to Tierra del Fuego) and higher parts of the Bolivian and Peruvian Andes (Lehmann, 1913).

The affinities between the species groups are rather obscure. Warren (1956: 390) writes: "It has been shown that the subdivision of *Issoria* is unjustified, the various types of the tenth abdominal segment testify to a close affinity which the world-wide distribution and complete segregation of many species has failed to obliterate". However, such a remark suggests that the groups are conjoined on account of the common possession of plesiomorphous character conditions, a poor basis for monophyly.

Although the phylogenetical affinities are obscure, the geographical affinities seem somewhat clearer. As related genera are absent in Africa but numerous in the Palaearctic Region, the African species group appears to be an Ethiopian offshoot of Palaearctic origin. Moreover, the most usual foodplants of the Palaearctic *Issoria* and related genera, *Viola* species, are also the foodplants of the Ethiopian species. The genus *Viola* is with 400 species mainly distributed in the temperate regions.

It seems possible that the Ethiopian and S. American groups are relics of an once larger, Holarctic group, driven away to outlying districts by a strong development of other (? new) genera (*Argynnis*, *Brenthis*, *Boloria*, etc.) in the Holarctic Region, or they could maintain themselves in Africa and S. America, because they had already colonized the mountains of these continents before more successful genera in the Holarctic almost completely replaced their parental stock.

*Melitaea*. One species, *abyssinica* Oberthür, belonging to the otherwise completely Palaearctic *didyma* group (27 species; Higgins, 1941) is the sole representative of this genus in the Ethiopian Region. It occurs in Ethiopia (Carpenter, 1935) and as a separate subspecies (*scotti* Higgins) in SW. Arabia (Gabriel, 1954).

*Ypthima*. This genus numbers more than 80 species in the Ethiopian, S. and E. Palaearctic and Oriental Regions, and a single species further east, in New Guinea and Australia (Common & Waterhouse, 1972). The only representative in the W. Palaearctic is *asterope* Klug. It is distributed throughout the Ethiopian Region, in wooded areas, bush, savanna, grasslands (Williams, 1969), and through Arabia and Syria to India, W. and C. China (Gabriel, 1954). As contrasted with what was claimed by Larsen (1974), *asterope* does not reach Australia (cf. Common & Waterhouse, 1972). In the W. Palaearctic, *asterope* occurs as far north as the Adana district in Turkey (Higgins, 1966; Larsen, 1974).

*Hipparchia*. There is some disagreement on the delimitation of this genus. It has many Palaearctic species. A single species, *tewfiki* Wiltshire, occurs in SW. Arabia (Gabriel, 1954), where it is endemic. Its closest relative is uncertain (possibly *statilinus* Hufn.), but in view of the distribution of the genus, *tewfiki* undoubtedly has a Palaearctic ancestor.

*Lasiommata*. Like the related genera, which formerly were united with this genus into the collective genus *Pararge*, *Lasiommata* is purely Palaearctic, except for two species, *felix* Warnecke, which is confined to SW. Arabia, and *maderakal* Guérin, an endemic species from Ethiopia (Fig. 2). Both species look very much like *maera* L., which extends from N. Africa and W. Europe to the Himalayas and De Lattin (1967) stated that these species are closely related. Indeed, I suppose the specificity of *felix* and *maderakal* is typologically, not biologically based.

*Virachola*. This genus, which could be considered a subgenus of *Deudorix*, is Indo-African and has 27 species in the Ethiopian Region (Stempffer, 1967). One of these species extends northwards into the Palaearctic:

*livia* Klug. — An eremic species, known from Tanzania, Somalia, Nubia, Arabia, Israel (Gabriel, 1954), and attaining its northern distribution limit in Lebanon (Larsen, 1974). It is migratory.

*Apharitis*. This genus was erected by Riley (1925) to receive nine eremic species, distributed from Ghana through the southern Sahara and Arabia to N. India. Their ranges are as follows (data from Riley, 1925, unless stated otherwise):

*gilletti* Riley. — Somalia.

*nilus* Hewitson. — S. Sudan to N. Nigeria and N. Ghana.

*buchanani* Rothschild. — N. Nigeria, S. Sahara.

*acamas* Klug. — C. Sahara (Ahaggar Mountains), Sudan, Egypt, SW. Arabia, north through Israel, Jordania and Lebanon to Cyprus and Taurus (Hemming, 1932; Larsen, 1974), east to Chitral.

*myrmecophila* Dumont. — Tunisia; Jordania and SE. Arabia (Hemming, 1932).

*epargyros* Eversmann. — Kurdistan to Baluchistan and northward to the Kirghis Steppes and Kuldja.

*cilissa* Lederer. — N. Syria, Kurdistan; Israel (Larsen, 1974).

*maxima* Staudinger. — N. Syria, Kurdistan.

*lilacinus* Moore. — Punjab to Assam.

From these data it appears that *Apharitis* is neither an Ethiopian nor a Palaearctic genus, but belongs to the eremic zone between the Ethiopian and Palaearctic Regions and penetrates into those regions.

*Tarucus*. This Indo-African genus was revised by Bethune-Baker (1918), who distinguished 20 species. Afterwards three species have been added. Stempffer (1967) lists 12 species from the Ethiopian Region. According to Clench (1965) "these small blues are essentially desert or subdesert species". Nevertheless, some species can live in the Palaearctic Region:

*theophrastus* Fabr. — From S. Spain through N. Africa, Turkey, Arabia and Iraq to India (Higgins & Riley, 1970), Burma and Ceylon (Swinhoe, 1905—10). In



Africa distributed from the Mediterranean to Senegal, N. Nigeria and Ethiopia (Clench, 1965).

*rosaceus* Austaut. — Algeria, Tunis, and desert oases in N. Africa and Arabia, widely distributed in W. Asia to Iraq and Iran (Higgins & Riley, 1970). In Africa *rosaceus* extends south to Senegal, N. Nigeria and Kenya (Clench, 1965).

*balkanicus* Freyer. — Coastal regions of Algeria and Tunis, and from the Adriatic coast through the Balkans and Turkey to Lebanon and Iran (Higgins & Riley, 1970). It also occurs in SW. Arabia (Gabriel, 1954). According to Larsen (1974) *balkanicus* occurs through "most of eremic Africa", but I have not found any confirmation of this statement.

The genus extends as far south as S. Africa, where three species occur (Swanepoel, 1953); in the Oriental Region it reaches Borneo.

*Lampides*. A monotypic genus. Its single species, *boeticus* L., is strongly migratory and occurs with little or no geographic variation throughout the hotter parts of the Old World. In the east it extends to Australia, where it is common (Common & Waterhouse, 1972) and since 1965 it has been found in New Zealand (Laidlaw, 1970). It is common throughout Africa and is found as a resident in S. Europe, but migrants have been observed as far north as N. Germany.

*Cyclyrius*. Only two species are placed in this genus, viz. *mandersi* Druce, which is confined to Mauritius, and *webbianus* Brullé, which flies in the Canary Islands. This peculiar and apparently relic distribution becomes somewhat more understandable if we know that *Cyclyrius* is thought to be closely related to the next genus, *Syntarucus* (see Stempffer, 1967; Eliot, 1973), which may have replaced *Cyclyrius* in continental Africa.

*Syntarucus*. Stempffer (1967) lists 11 species from the Ethiopian Region, five of which are restricted to islands. In the Oriental Region a single species, *plinius* Fabr., occurs, from India to Java (Swinhoe, 1910—11; Wynter-Blyth, 1957). One of the Ethiopian species, *pirithous* L., is also found (subspecifically indistinct) throughout S. Europe and much of Turkey. Larsen (1974) considered it an "Afro-eremial species", but it is certainly not strictly "eremial". According to Boorman (1970), it is a common species of forest and savanna areas in W. Africa, and Swanepoel (1953) states that *pirithous* (he used the junior synonym *telicanus*) occurs literally everywhere in S. Africa.

It is interesting to note that no *Syntarucus* species are known from the Canary Islands and Mauritius, where the *Cyclyrius* species are found, although many islands around Africa have been colonized by *Syntarucus* species.

*Chilades*. There appears to be much disagreement on the delimitation of this genus, also in recent times. Clench (1965) stated: "This small genus of about eight species, most of which are Australian, has two species occurring in Africa. . .". Stempffer (1967) placed seven Ethiopian species in this genus, although he, in the description of the genus *Freyeria*, stated that *Chilades* occurs from Egypt to the New Hebrides. However, neither D'Abrera (1971) nor Common & Waterhouse (1972) mentioned this genus from the Australian Region. There is only a single Oriental species of which I am sure, viz. *laius* Cramer, as it is the type species of

the genus; it occurs in India, Ceylon, Burma and S. China (Swinhoe, 1905—10).

A single species, *galba* Lederer, is found in the Palaearctic Region. It is confined to the Middle East and has been found in S. Turkey, Lebanon, Jordan, Israel, Arabia, Iraq (Larsen, 1974). According to Wiltshire (1957), it is an oasis and desert insect. Due to the chaotic classification of *Chilades*, it is impossible to state whether *galba* is more closely related to Ethiopian or to Oriental species.

*Freyeria*. As with the foregoing genus it is obscure which species can be assigned to this genus. In Africa there are two species (Stempffer, 1967). One of them is confined to Madagascar (*minuscula* Aurivillius), the other (*trochilus* Freyer) is widespread in the Ethiopian Region, occurring in the savannas from W. to E. Africa and southwards to the Cape; it is also known from S. Cameroon and Gabon (Clench, 1965). Outside the Ethiopian Region *trochilus* flies from Egypt and Arabia to Ferghana and through the Oriental Region to the Philippines and Australia (Common & Waterhouse, 1972). In the W. Palaearctic it occurs through Lebanon and Iraq north to Turkey and the Balkans. In Europe it is found on barren stony ground (Higgins & Riley, 1970), and Larsen (1974) and Wiltshire (1957) mention comparable habitats in Lebanon and Iraq.

*Azanus*. Another Lycaenid genus common to the Ethiopian and Oriental Regions. Stempffer (1967) records seven Ethiopian species, while four species are mentioned by Swinhoe (1910—11) from India to Sumatra. One of these species, *jesous* Guérin, occurs in the Palaearctic, in addition to an Afro-Oriental distribution. Its distribution is as follows: Ethiopia to the Cape, Madagascar; in N. Africa in Morocco and Egypt; Arabia to Lebanon; further east in India, Ceylon and Burma (Higgins & Riley, 1970; Larsen, 1974; Wynter-Blyth, 1957). Larsen called it an Afro-eremic species, but he was probably unaware of its occurrence in the Oriental Region.

*Zizeeria*. A small genus of four or five species (Chapman, 1910; Common & Waterhouse, 1972); two species are confined to the Oriental Region, one to the Australian Region, and the fourth, *knysna* Trimen, is palaeotropical, occurring from S. Africa to Oceania. This widespread species is also found in the W. Palaearctic (Fig. 8). It can be divided into two forms, which only differ in the male genitalia and are, by some authors, considered separate species. These forms are:

*knysna* Trimen. — Throughout the Ethiopian Region, including Madagascar, Mauritius, Seychelles, north to SW. Arabia in the east (Gabriel, 1954), to Canary Islands and through Algeria and Morocco to northern Spain (Gomez Bustillo & Rubio, 1974) in the west.

*karsandra* Moore. — E. Algeria, Tunisia, Sicily, Crete (Higgins & Riley, 1970) and from Lebanon to Oceania (Larsen, 1974) and Australia (Common & Waterhouse, 1972).

The habitat of this species is described by Higgins & Riley (1970) as "moist places beside streams", and Wiltshire (1957) observes that "it is not a desert insect, and favours roadsides, paths, lawns and gardens, though not exclusive to such".

*Lycaena*. There is some disagreement on the subdivision of this genus. In its broadest sense it comprises about 30 Palaearctic (Kostrowicki, 1969) and 16

Nearctic species (Dos Passos, 1964). It is not exclusively Holarctic: there is one species in the mountains of Guatemala, three species occur completely inexplicably in New Zealand (Laidlaw, 1970), and there is a slight Ethiopian representation.

Verity (1943) needed six genera to class the Palaearctic species and his classification was largely, but not entirely, adopted by Higgins & Riley (1970) so far as the European species are concerned. The Ethiopian representatives belong to *Lycaena* s.s., which has about ten Palaearctic species and a number of Nearctic ones. The Ethiopian species are (Fig. 4):

*phlaeas* L. — Its range comprises almost all of the Holarctic Region. It is a very adaptable species; in the Palaearctic *phlaeas* is found from the oases in the desert-like plains of Iraq (Wiltshire, 1957) to the shore of the Arctic Sea in Norway (Nordström, 1955). In the Ethiopian Region it occurs above 2000 m in SW. Arabia (ssp. *shima* Gabriel) and in the mountains of Ethiopia (ssp. *pseudophlaeas* Lucas).

*abottii* Holland. — Confined to the highlands of Kenya and N. Tanzania, where it flies in grassy places along streams, etc. The larvae feed on *Rumex* (Williams, 1969), one of the foodplants of *phlaeas*. According to Stempffer (1967), *abottii* could be a subspecies of *phlaeas*.

*orus* Cramer. — Restricted to S. Africa, where it inhabits the south-western and southern coastal regions as far as Port Elizabeth; it occurs from sea level up to moderate altitude; the larvae feed on *Polygonum* (Clark & Dickson, 1971), one of the foodplants of *phlaeas*.

*clarki* Dickson. — Also restricted to S. Africa, where it is mainly an inland insect (Clark & Dickson, 1971). Up to 1971 it was considered conspecific with *orus* and the remarks by Swanepoel (1953) about the habitat of *orus* ("a highland butterfly occurring mostly in places where winter is most severe") may refer to *clarki*. The larvae of *clarki* feed on *Rumex* (cf. *abottii* and *orus*).

With regard to the southern extensions of the otherwise Holarctic genus *Lycaena* s.l., Stempffer (1967) remarked: "One can understand how, during the colder geographical [I suppose he meant geological] periods, the genus *Lycaena* managed to reach South Africa by way of the mountains of Abyssinia and East Africa. It is much more difficult to explain how it reached New Zealand, since in Asia it extends no further than the Himalayas and Sze Chuan being effectively replaced by *Heliophorus* in further Asia".

*Carcharodus*. In its broadest sense this genus comprises about six Palaearctic species; in its most restricted sense it is monotypic, its single species, *alceae* Esper, occurring through most of the western part of the Palaearctic Region, east to C. Asia and N. India. In SW. Arabia it is found as a separate subspecies, *wissmanni* Warnecke.

*Spialia*. The 27 species of this genus can be classified into seven species groups, which all occur in the Ethiopian Region, while three groups are also represented outside this area (De Jong, 1974b, and in press). Two groups have members in the West Palaearctic Region:

*sertorius* group (Fig. 10). — Comprised of the species *mafa* Trimen (from S. Africa through E. Africa north to Ethiopia and SW. Arabia), *sertorius* Ochs. (W. Europe and NW. Africa), *orbifer* H.-S. (E. Europe to E. Asia) and *galba* Fabr.

(India to Ceylon and Burma; Hainan). The Palaearctic members, *sertorius* and *orbifer*, are supposed to be the northern offshoot of an originally Ethiopian stock; both can be divided into a number of geographic forms which are believed to reflect the isolation during glacial periods (De Jong, 1974b). The species of this group can usually be found in hot localities, in open and flowery places; I found *mafa* in Kenya up to an altitude of 2000 m.

*phlomidis* group. — Mainly distributed in the dry regions bordering the desert belt that separates the Palaearctic and Ethiopian Regions. Three species are confined to the region north of the desert belt, viz. *phlomidis* H.-S., *osthelderi* Pfeiffer, and *geron* Püngeler, while the fourth species of this group, *doris* Walker, is found to the north and south of this zone and is, virtually, capable of living in the desert, as far as its foodplant, *Convolvulus lanatus*, grows. In the Ethiopian Region *doris* is known from Sudan, Ethiopia and Somalia. It also occurs in SW. Arabia. In the Palaearctic Region *doris* is found in Morocco and from Egypt to Pakistan. Mainly on the basis of its genitalia *doris* is supposed to be the most recent member of the group (De Jong, 1974b). Although there appears to be a close relationship with the Ethiopian *spio* group, it cannot be stated that the *phlomidis* group has an Ethiopian origin (see also Chapter 3, Summary and conclusions, p. 185). As *doris* seems to be the most recent member of the group and its relatives are Palaearctic, it is concluded that *doris* invaded SW. Arabia and E. Africa from the north.

*Gegenes*. A small genus of four species. Two species, *niso* L. and *hottentota* Latr., are restricted to the Ethiopian Region, where they are widely distributed; one, *nostrodamus* Fabr., is distributed disjunctly around the Mediterranean, eastward to NW. India and southward to Aden, Omdurman and Kassala, and the fourth, *pumilio* Hoffm., is found over the combined areas of its congeners, but is lacking from Tunisia to the Sinai. All species are usually met with in hot and dry localities, and *nostrodamus* and *pumilio* appear to be the most eremic species, which may count for the fact that they occur in the Palaearctic as well as the Ethiopian Region and have a patchy distribution around the Mediterranean. Although the Ethiopian species (*hottentota* and *niso*) can live in dry conditions, they are usually found in more or less grassy places. Indeed, in E. Africa *niso* is perhaps the commonest species of HesperIIDae and I found it in Kenya most numerous along paths in more or less wooded areas. Possibly their preference for grassy places has forced *niso* and *hottentota* to remain restricted to Africa south of the Sahara.

Recently, Larsen (in litt.) found differences between the East and West Mediterranean *pumilio* populations and he thinks these populations to be specifically distinct. This interesting observation has also some bearing on the reconstruction of the geographic history of the genus. On the (unfirm) basis of the distribution of related genera (cf. Evans, 1937, 1949) I have concluded that the genus originally formed part of the old, Tertiary steppe fauna that invaded Africa from the east. As the extant species seem to fall apart into two groups, viz. *pumilio/nostrodamus* and *niso/hottentota*, there appears to have been an Ethiopian and a South Palaearctic development of the genus, which may have been initiated by the desiccation of the area that is now covered by the Saharo-Arabian desert. In this reconstruction the differentiation of *pumilio* in the Mediterranean area may

be the result of glacial isolations, and both *pumilio* and *nostrodamus* are northern invaders in Africa.

An alternative hypothesis, adhered to by Larsen, assumes that *pumilio* is an Ethiopian species that invaded the Mediterranean along two routes, giving rise to an East and a West Mediterranean form. If the ancestor of the *pumilio/nostrodamus* stock was Ethiopian, also *nostrodamus* is an Ethiopian element in the Palaearctic and one could imagine that *Gegenes* expanded twice to the Mediterranean, the first time bringing the ancestor of *nostrodamus* to the north, the second time giving rise to the two different *pumilio* forms. This reconstruction sounds very plausible, but does not take into account that the *pumilio/nostrodamus* ancestor must have originated somehow and somewhere. As the *Gegenes* species can live in steppe-like habitats, the genus has undoubtedly formed part of the steppe fauna that in Tertiary times was distributed from Africa to India, whatever the geographic origin of the *Gegenes* ancestor. In that case, however, it is much more easily imaginable that *pumilio/nostrodamus* originated north than south of the Sahara (see above). Consequently, I consider provisionally both *pumilio* and *nostrodamus* northern invaders in Africa. I cannot consider the wide distribution of *pumilio* south of the Sahara (ssp. *gambica* Mab.) an objection to this hypothesis, for why should not a steppe species expand itself so widely over Africa?

*Borbo*. A palaetropical genus; 17 species are restricted to the Ethiopian Region, three are only found in the Indo-Australian area, and one species, *borbonica* Boisd., is distributed throughout the Ethiopian Region, in Madagascar and various islands in the Indian Ocean (Bourbon is type locality), in N. Africa (Morocco, Algeria, Egypt), the Middle East (Syria, Lebanon, Israel), and is also found in Spain, in Gibraltar and Tarragona (Gomez Bustillo & Rubio, 1974). The Mediterranean populations have been distinguished as ssp. *zelleri* Lederer. *B. borbonica* is a rather eclectic species which can live in eremic as well as in more humid and wooded areas. I found it in W. Kenya along paths in the Kakamega Forest.

*Pelopidas*. This genus is mainly Indo-Australian, but among its nine species two (*mathias* F. and *thrax* Hbn.) are found in the Ethiopian as well as in the Oriental Region and these species are the sole representatives of the genus in Africa. Only *thrax* reaches the W. Palaearctic: Turkey (Higgins, 1966), Syria, Lebanon (Larsen, 1974), Jordan (Hemming, 1932), Cyprus, Israel (Evans, 1949); further from Egypt through Arabia and Iraq to NW. India, Burma and Malaya (Evans, 1949), and through most of the Ethiopian Region (Evans, 1937). In the W. Palaearctic the same subspecies (ssp. *thrax* F.) occurs as in NW. India, the Ethiopian subspecies is different (ssp. *inconspicua* Bertolini). It is a known migrant (Larsen, 1974), but that does not mean that it is not resident in the W. Palaearctic. As *B. borbonica*, *thrax* seems to be a species that has not a very restricted habitat preference.

### 3. THE AFFINITIES BETWEEN THE WEST PALAEARCTIC AND ETHIOPIAN BUTTERFLY FAUNAS

From the data given in Chapter 2 it is obvious that the Palaearctic-Ethiopian affinity cannot be simply described as a north-south connection, but that it is of a

rather complex nature. In this chapter we will try to unravel the various types of affinities. The first division to be made is into direct and indirect affinities.

The term "direct affinity" is applied to those cases which concern a penetration from region A into region B, disregarding a possible secondary radiation in region B. In the present instance two such direct affinities are possible, viz. a penetration from the Palaearctic into the Ethiopian Region and vice versa.

By the term "indirect affinity" is meant that region A or B, or both, received the taxon which it has in common with the other region, from a source outside the other region. In some cases this source can be indicated (allowing a subdivision of this category), in other cases taxa are placed under this heading by lack of knowledge. 7

### Direct affinities

#### Palaearctic influence in the Ethiopian Region

The species of this group are listed in Table 2. Some features of this group are:

a. all species belong to genera which are not represented in the Oriental Region, or at most penetrate slightly into that region (*Pieris*, *Colias*, *Gegenes*);

Table 2. Species of (ultimately) Palaearctic origin in the Ethiopian Region. An asterisk indicates that the species is not specifically distinct from Palaearctic species

	SW. Arabia	E. Africa	S. Africa
<i>Pieris brassicoides</i>		x	
* <i>Pontia daplidice</i>	x	x	
* <i>glauconome</i>	x	x	
<i>distorta</i>		x	
<i>helice</i>		x	x
* <i>Euchloe belemia</i>		x	
* <i>falloui</i>	x	x	
* <i>Colias erate</i>	x	x	
<i>electo</i>	x	x	x
<i>Issoria hamingtoni</i>		x	
<i>smaragdifera</i>		x	
<i>excelsior</i>		x	
<i>Melitaea abyssinica</i>	x	x	
<i>Hipparchia tewfikii</i>	x		
<i>Lasiommata maderakel</i>		x	
<i>felix</i>	x		
* <i>Tarucus balkanicus</i>	x		
* <i>Lycaena phlaeas</i>	x	x	
<i>abottii</i>		x	
<i>orus</i>			x
<i>clarki</i>			x
* <i>Carcharodus alceae</i>	x		
* <i>Spialia dorus</i>	x	x	
* <i>Gegenes nestrodamus</i>	x	1)	
* <i>pumilio</i>		x	x

1) occurs in Sudan

b. most Ethiopian representatives are conspecific with Palaearctic species or are so closely related that they can be considered to form a superspecies together with Palaearctic species;

c. in the Ethiopian Region most species are confined to the north-eastern, eastern and/or southern part, and no species are confined to W. Africa;

d. none of the species are forest species, though they may fly in close proximity to the forest; for the rest, their habitat preferences are divergent, ranging from eremic (e.g., *Euchloe falloui*) to montane grasslands (e.g., *Pieris brassicoides*).

### Ethiopian influence in the Palaearctic Region

There is only a small number of originally Ethiopian species occurring in the Palaearctic Region, but as will be shown it is impossible to delimit this group precisely. The species are listed in Table 3. Their common features are:

a. all species belong to genera which have at least one endemic species in the Oriental Region;

b. all species fly north as well as south of the Sahara and the northern populations are usually subspecifically not differentiated from the southern ones (*Spialia sertorius* and *orbifer* are exceptions; they are considered to form a superspecies with the Ethiopian *mafa* and the Oriental *galba*);

c. in the Palaearctic the species are confined to the Mediterranean area (again, *Spialia sertorius* and *orbifer* are exceptions);

d. they are no forest species, but for the rest their habitat preference is divergent. Generally speaking the species live in Africa in various types of savanna country. The pierid and lycaenid species are the most eremic ones.

Table 3. Species in the Palaearctic Region originating from the Ethiopian Region. An asterisk indicates that the species is not specifically distinct from its Ethiopian relative, two asterisks indicate that the species occurs with different subspecies in the Palaearctic and Ethiopian Regions

	West Mediterranean	East Mediterranean
** <i>Colotis evagore</i>	x	
* <i>calais</i>		x
* <i>chrysonome</i>		x
* <i>Catopsilia florella</i> p.p.	<sup>1)</sup>	<sup>2)</sup>
* <i>Danaus chrysippus alcippus</i>	x	<sup>2)</sup>
** <i>Charaxes jasius</i>	x	x
* <i>Virachola livia</i>		x
* <i>Syntarucus pirithous</i>	x	x
* <i>Zizeera knysna knysna</i>	x	<sup>2)</sup>
<i>Spialia sertorius</i>	x	
<i>orbifer</i>		x
** <i>Borbo borbonica</i>	x	x

<sup>1)</sup> only in Canary Islands

<sup>2)</sup> see Table 4

Of the listed species we can be reasonably sure that they are Ethiopian intruders in the Palaearctic Region, as they otherwise occur only in Africa (except *Spialia*). Among the species listed in Table 3, four have an Indo-African distribution. Their

Ethiopian origin has been concluded from their geographic variation, except *Catopsilia florella*, which has no subspecies and of which the Canary Islands population can only have originated from W. Africa. There are, however, more species with an Indo-African distribution which also occur in the Palaearctic Region, but without a subspecific indication as to their geographic origin. For that reason they will be dealt with in the next paragraph.

### Indirect affinities

#### Indo-Ethiopian and eremic species

As it appears impossible to divide sharply between species with an Indo-Ethiopian and an eremic distribution, these species (so far they occur in the Palaearctic Region) have been listed together in Table 4. Their common feature is

Table 4. Species in the Palaearctic Region with an Indo-Ethiopian or eremic distribution

	W. Medi- terranean	E. Medi- terranean	Africa S. of equator	migratory
<i>Colotis phisadia</i>		x		
<i>fausta</i>		x		x
<i>Anaphaeis aurota</i>		x	x	x
<i>Catopsilia florella</i>		x	x	x
<i>Danaus chrysippus chrysippus</i>	1)	x	x	x
<i>Hypolimnas misippus</i>		x	x	x
<i>Precis orithya</i>		x	x	x
<i>Ypthima asterope</i>		x	x	
<i>Apharitis acamas</i>		x		
<i>myrmecophila</i>	x	x		
<i>Tarucus theophrastus</i>	x	x		
<i>rosaceus</i>	x	x		
<i>Lampides boeticus</i>	x	x	x	x
<i>Chilades galba</i>		x		
<i>Freyeria trochilus</i>		x	x	
<i>Azanus jesous</i>	x	x	x	
<i>Zizeeria knysna karsandra</i>	x	x	2)	
<i>Pelopidas thrax thrax</i>		x	x	x

1) see also Table 3

2) in the Ethiopian Region only *Z. knysna knysna*

that it is improbable that they have an Ethiopian or Palaearctic origin. For some species (*Colotis fausta*, *Pelopidas thrax*) an Oriental origin appears obvious. For other species the region of origin is quite uncertain and it is possible that all species belong to the fauna that has always lived in the contact area between the Palaearctic, Oriental and Ethiopian Regions, not a mixed fauna, but a more or less independent, intermediate fauna (without sharp boundaries). This is most obvious in the eremic species, as they are confined to the said region. The less confined to an eremic habitat, the larger is the distribution, and some species can live in such a variety of habitats, including the eremic, that they could extend their range throughout the warmer parts of the Old World (e.g., *Danaus chrysippus*,



*Hypolimnas misippus*, *Lampides boeticus*). Whatever their place of origin, none of these species can now be considered a Palaearctic intruder in Africa or an Ethiopian intruder in Eurasia.

Two other features call for attention, viz. the small number of species of this category in the W. Mediterranean and the large number of migratory species. The latter feature may be partly responsible for the slight subspecific differentiation of the species. The occurrence of two of these species in the W. Mediterranean, viz. *Catopsilia florella* and *Danaus chrysippus chrysippus*, appears to be a direct result of their migratory habit. Apart from these two species only five species of Table 4 occur in the W. Mediterranean, while all species are known from the E. Mediterranean (none of the species occurs outside the Mediterranean except the migratory *Lampides boeticus*). A possible historical explanation for this difference is given in Chapter 4.

### Remaining genera

Five genera remain to be dealt with. Two of them, viz. *Papilio* and *Neptis*, are very rich in species in tropical environments, while few species occur in temperate regions. Whatever their geographic history may have been, there are no indications that they crossed the eremic zone between the Palaearctic and Ethiopian Regions in more or less recent times as no species occur north as well as south of the Saharo-Arabian desert zone. It is possible, if not probable, that the W. Palaearctic members of these genera are originally invaders from the E. Palaearctic (and neighbouring Oriental) Region.

The distributions of the genera *Libythea* and *Cyclyrius* show a relict character and little or nothing can be said on their history.

The genus *Vanessa* is the only one in this group that has the same species (*cardui*) flying in both the Palaearctic and Ethiopian Regions. Although this very strongly migratory species seems to cross the Sahara rather regularly to the north, it is very unlikely that it should be considered an Ethiopian intruder in Europe. Although its geographic origin is uncertain, it may be suggested that *cardui* is a New World species that by its strong migratory behaviour conquered the world.

### Summary and conclusions

Summarizing, four kinds of relationship between the West Palaearctic and Ethiopian Regions can be distinguished:

- a. by southward traverse across the Saharo-Arabian desert zone,
- b. by northward traverse across the Saharo-Arabian desert zone,
- c. through the Oriental Region,
- d. through the eremic fauna.

Apparently the Sahara has been successfully crossed several times by various species, from north to south and vice versa. Taking the view that generally speaking the existence of species common to the regions north and south of the Sahara indicates a more recent contact than that of common genera without common species, the traverses seem to cover a long period. The more remarkable

is the very small number of successful traverses. Successful north-south traverses number about 17 (cf. Table 2) and most traverses are of such a recent age that the species concerned scarcely had time for differentiation (although only ten originally Palaearctic species in the Ethiopian Region are considered conspecific with Palaearctic species). If we bear in mind that the West Palaearctic comprises more than 400 butterfly species, it is apparent that the Sahara is an efficient barrier for the West Palaearctic butterfly fauna in general.

For the Ethiopian butterflies the Sahara appears to act as a still stronger barrier. Successful northward traverses number only twelve (cf. Table 3). As the Ethiopian butterfly fauna comprises almost 2700 species, it is evident that a successful crossing is a very rare event (but in Chapter 4 it will be shown that unsuccessful crossings may have been rather frequent). In all cases the same species occurs north as well as south of the desert zone and the species are confined in the Palaearctic to the Mediterranean (with the exception of *Spialia sertorius/orbifer*). This suggests that the average age of the northward traverses is still younger than that of the southward ones.

Thus there appear to exist two remarkable differences between the southward and northward traverses, viz.:

a. in relation to the total number of butterfly species in the West Palaearctic and Ethiopian Regions the southward traverses are much more frequent than the northward ones;

b. judged from the differentiation of the species after the traverse the southward traverses cover a much longer period than the northward ones.

A possible explanation for these differences is given in the next chapter.

The Indo-Ethiopian genera pose a separate problem. Not all of these genera have representatives in the W. Palaearctic. The complex nature of the Indo-Ethiopian relationship falls outside the scope of this paper, but in the next chapter a few words have to be said on this subject in order to get a better insight in the Euro-Ethiopian affinities.

#### 4. HISTORICAL ASPECTS

In this chapter we will try to relate the data amassed in the foregoing chapters to ecological changes in the northern part of Africa in the past. As the Euro-Ethiopian affinities in the butterflies are mainly at the species level, we are primarily interested in the ecological changes that took place during the Pleistocene. Affinities at the genus level may point to an older, Tertiary connection. Very little is known of this period and various authors do not always agree. Nevertheless, the little that is known may help to explain the distribution patterns found.

Ecological history of the northern half of Africa and the Arabian peninsula

##### Tertiary

For our purpose it does not seem relevant to consider the period prior to the Miocene as it is hardly believable that a contact broken since then is at present still discernible at the genus level.

From Middle Miocene to Late Pliocene there was a connection with the Oriental Region via Arabia. The Red Sea in its present form came into existence only at the end of the Pliocene or the beginning of the Pleistocene; prior to that time it was a large inland sea (Ekman, 1953). As the Persian Gulf also appears to be rather recent and the climate in this area in Miocene and Pliocene was often more humid than at present (e.g., at the end of the Miocene and various times in the Pliocene Egypt has experienced periods of considerable rainfall, see Moreau, 1952), a close contact between and intermingling of the Oriental and Ethiopian faunas was possible. This intermingling was largely unidirectional and consisted mainly in a large invasion of Oriental faunas (De Lattin, 1967). In the Pliocene the correspondence has been still larger than at present, as many groups became extinct in the Oriental Region (shown by the famous fossil Siwalik fauna of N. India).

I wonder if it is correct to speak of Oriental species invading Africa, as is usually done. It concerns mainly steppe species which lived in a region that is now partly Oriental, partly Palaearctic. The uplift of the Himalayas (of which the Siwalik Range forms the southern border), the main boundary between the Palaearctic and Oriental Regions, "is believed (...) to have taken place in four major impulses, respectively during the Eocene, the Middle Miocene, the Upper Pliocene and in the Late Pleistocene" (Mani, 1968). This means that it is not relevant to speak of a Palaearctic and an Oriental Region as biogeographical regions in the Tertiary. Thus, it is misleading to speak of an Oriental invasion into Africa, and it seems more suitable to term it an Asiatic invasion.

More temperate Asiatic species, especially those which could not live in a steppe or savanna environment, had at this period no chance of reaching Africa as the mountains by way of which they could cross the steppe region were still in the process of uplifting and there were not yet mountains in East Africa high enough to support temperate species.

The progress of the Alpine orogeny in Late Tertiary and especially the gradual rise of the Taurus-Armenia-Zagros mountain system, the falling temperature and the opening of the southern end of the Red Sea (not before the middle of the Pliocene; Ekman, 1953), must have hampered the free exchange of steppe species between Asia and Africa. Nevertheless, during humid periods the passage, though difficult, must have been possible.

There is no full agreement on the Tertiary connections between Africa and Europe in the W. Mediterranean. According to Moreau (1966) there was a landbridge in the Tunisia-Sicily area in the Pliocene. Besides such a landbridge Verity (1940) mentioned a direct connection between Sardegna and Africa in the early Pliocene, but it is not clear how far such a connection is supported by geological evidence.

Although Moreau (1966) stated that there is no evidence of a connection across the Straits of Gibraltar, Ekman (1953) postulated a Middle Tertiary landbridge between Cape Spartel and Cape Trafalgar, although in the Pliocene the Mediterranean became connected to the Atlantic, subsequently through the valley of the Guadalquivir, the valley of Fez and at last across the Straits of Gibraltar. A similar sequence of events was given by Verity (1940) and Kostrowicki (1969). It is

clear that such a connection in this area cannot have been of much importance as a direct passage, as only those species occurring in the northernmost tip of NW. Africa when it was conjoined to Spain, could freely move into Africa when this part became connected to the rest of NW. Africa. But apart from such a connection, the Straits of Gibraltar are only a narrow gap (at present 13 km), and anyone who from Tarifa, the southernmost point of Spain, has looked at the mountains of Tanger will be convinced that in due course many species must have been able to cross the gap.

In the meantime the Atlas Mountains were uplifted, rendering temperate species a possible habitat far to the south. However, during the Tertiary the lowland was probably still too warm to give temperate species the opportunity to expand to the south. Moreover, the Sahara south of the Atlas Mountains would have been a strong barrier for temperate species, although it may have been covered over large areas by mediterranean shrub and savanna-like vegetation, possibly continuously so along the Atlantic coast to the W. African savannas. But warmth-loving species of open formations may have been able to cross the Sahara by this way (to the north as well as to the south), thus forming a connection between the European and Ethiopian faunas.

In sum, interchange of species between the W. Palearctic and Ethiopian Regions during the Miocene and Pliocene was possible through Arabia and the Middle East and, probably to a lesser extent, across the W. Mediterranean and through NW. Africa. Only species which could live in a steppe or savanna-like environment could make use of these connections.

The above description suggests that we know a lot of the Late Tertiary ecology in the area concerned, but considering that this period covered about 25 millions of years during which large mountain massifs were uplifted and ecological conditions must have changed at a large scale, it is clear that we know extremely little.

### Pleistocene

About the relatively short Pleistocene period (about 2 millions of years; considered here to extend up to the present day, after Moreau, 1966, and Hamilton, 1974) we are rather better informed, though most data refer to the last 30,000 years.

The glaciations of the Palearctic brought many temperate species far to the south where they could survive warmer interglacial periods in the S. Palearctic mountains. Thus, an ecologically wider array of species stood, as it were, waiting to cross the Sahara as soon as conditions became favourable.

At present the Sahara is too dry to be crossed by Palearctic as well as Ethiopian species. During a more humid period an interchange of species living in steppe and savanna and perhaps mediterranean shrub would be possible, but for species not capable of living in such an environment a lower temperature is required. Recent investigations, particularly pollen analysis, have revealed that there have, indeed, been colder and more humid periods. The history of the vegetation of East Africa was summarized by Van Zinderen Bakker (1971) and Hamilton (1974). It appears that from 30,000 to 25,000 BP (Kalambo Interstadial,

corresponding with the European Paudorf Interstadial) the temperature was about 2° C lower than at present. The temperature decreased between 25,000 and 12,500 BP to 6° C lower than now. This period is known as the Kenya Glacial and coincides with the last maximum of the Würm Glaciation in the Palaearctic. After a rapid increase the temperature c. 10,500 BP was similar to today. A further synchronization in the temperature fluctuation between Europe and East Africa is the occurrence of a short cold phase just before the Postglacial Climatic Optimum, about 4500—7500 BP (Neolithic), when temperatures were about 2° C higher than today.

This synchronization suggests that similar fluctuations took place in the intervening area. This is very important. The lower limit of the montane zone in East Africa, at present at 1500 m, is supposed to have been depressed at least by 1000 m during the maximum of the Kenya Glacial and Moreau (1966) calculated that even only 12,000 BP, with a temperature 2.5° C lower than today, the lower montane limit would have been at 1000 m. If we suppose that a similar descent of the montane zone took place in the area between East Africa and the Palaearctic, the enormous impact on the distribution of montane habitats is easily seen from the surface relief shown in Fig. 1. In fact an almost continuous montane block was

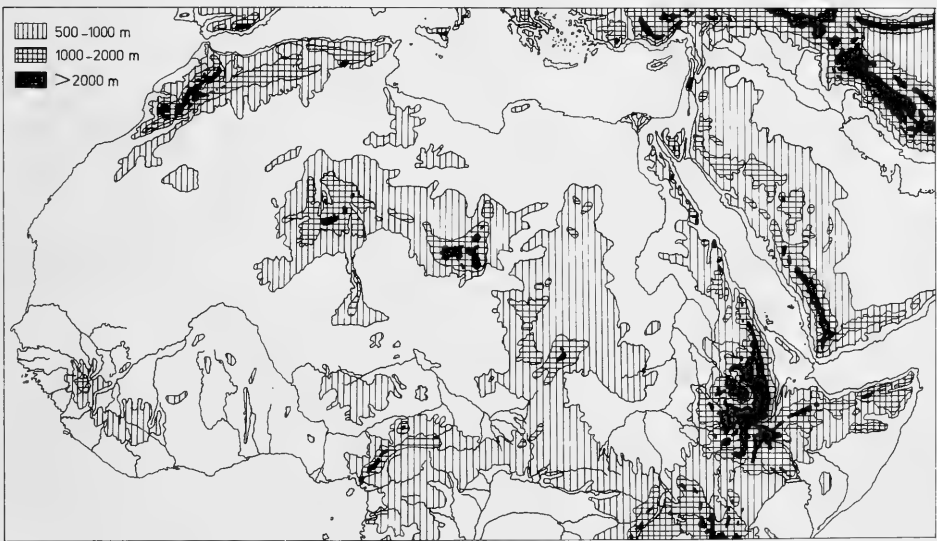


Fig. 1. Surface relief in northern Africa

formed from Asia Minor to East Africa, and from NW. Africa diagonally across the Sahara to Central Africa. Indeed, pollen analysis has shown that the Ahaggar Massif during much of the later part of the last glaciation was clothed with a rich mediterranean vegetation and even the European lime (*Tilia*), now absent in N. Africa, occurred there (Moreau, 1966).

There is, however, one factor which must have greatly influenced the availability of montane habitats for Palaearctic species trying to extend their range

southward, viz. humidity. Hamilton (1974) observed, that at least in the East African mountains the last glacial was dry, contrary to the common opinion that it was a pluvial period. Moreover, according to Moreau (1966) Arabia has probably never been better than semiarid at any time during the Pleistocene, except the mountain areas of Yemen and Gebel Akhdar and the somewhat elevated southern rim of Arabia, where wooded steppe and savanna may have existed, possibly with patches of dry evergreen forest, during glaciations and the humid Neolithic.

Although the duration, extension and chronology of dry and humid periods are still largely unknown, it is clear that drought must have hampered the southward extension of Palaearctic species, if it occurred during the only periods the temperature was low enough for such an extension, i.e. during glacial periods.

For Ethiopian species trying to extend their range northward, drought as well as low temperatures would have been unfavourable. How far the warm interglacial periods have been favourable for northward extensions is unknown at present (apart from a humid period in the latter Middle Pleistocene; Moreau, 1963), but at least postglacially there has been a favourable period, viz. the humid period during the Neolithic, in Europe known as the Postglacial Climatic Optimum or the Atlantic (cf. Moreau, 1955). This humid period, with a temperature about 2° C higher than now, attained its maximum about 5,000 years BP. At that time the western Sahara (and also the mountains of Aïr and Tibesti) was covered by mediterranean vegetation (scrub and dry woodland) up to the southern limit of the present Sahara, where it was in contact with the Ethiopian savanna vegetation (Moreau, 1966). Braestrup (1947) pictured the rivers at that time running across the western Sahara. It is clear that especially the coastal belt along the Atlantic requires only a small degree of climatic improvement in order to become viable as a passage for northern and southern species. The area north-east of the line Tripoli-Khartoum, however, appears to have always been drier and during the Neolithic only the Nile Valley could act as a corridor in this area (Moreau, 1963). However, the Neolithic period is believed to have been humid in the Sudan and Ethiopia and Moreau (1966) mentioned for Arabia, at least for its southern part, a somewhat richer vegetation, especially in mountainous areas, during this period.

For temperate Palaearctic species trying to go southward the Postglacial Climatic Optimum must have been a bad period. As a consequence of the higher temperature (about 2° C) the lower limit of the montane zone was about 400 m higher. Mountains below 1900 m lost their montane habitat and their function as stepping stones, montane habitats became more isolated and the land in between too hot.

By a sudden deterioration late in the Neolithic, caused by unknown factors, the entire mediterranean vegetation in the western part of the Sahara became extinct and from that time on the present bare condition of the western Sahara was developed. A similar condition has existed earlier in the Pleistocene, as at some stage in the late Pleistocene, prior to 22,000 BP the dunes of the Sahara extended even 300 miles south of the present limit of moving sands in West Africa. It is obvious that the present and similar conditions do not facilitate the passage in both directions.

To summarize the Pleistocene vicissitudes, it can be said that during glaciations,

conditions were favourable for a southward traverse, as far as drought did not prevent it. For the last time such conditions existed from about 25,000 to 18,000 BP. Northward traverses were mostly feasible during humid periods, the last of which occurred only about 5000 BP.

The distribution of mountain ranges suggests that the route from the Middle East to the Ethiopian highlands and further south was much easier for temperate species than from the NW. African mountains southward. It is not clear whether a western or an eastern traverse was easier for Mediterranean and Ethiopian species; possibly both traverses were equally easy (or difficult), though not necessarily at the same time.

### The direct West Palaearctic - Ethiopian affinities

#### The southward traverse

The Palaearctic species in the Ethiopian Region are largely absent from West Africa, suggesting that these species used mainly the eastern traverse. It should, however, be borne in mind, that East Africa offers the best opportunities for more or less temperate species to survive in its large mountain areas, and the possibility that also the western traverse was used but the species became extinct there, cannot be ruled out in advance. Indeed, there are indications that some species crossed the Sahara in its western part, but if they ever reached the Ethiopian Region, they died out entirely there. The southward movement in the western traverse is shown by the species at present occurring in the mountain areas in the Central Sahara, viz. Ahaggar (3000 m), Aïr (2000 m), and Tibesti (almost 3500 m). Table 5 gives an impression of the butterfly composition of these mountains. Although the data of these areas are incomplete, it is remarkable that in Tibesti, at the greatest distance from the Atlas Mountains, still six species of the families Pieridae and Nymphalidae occur that can be considered northern immigrants. Bernardi (1962) also listed *Vanessa cardui* as a Palaearctic species in Tibesti, but to me the geographic history of *cardui* seems obscure; moreover, the lack of subspecific variation makes it impossible to decide on the origin of the Tibesti population.

Four out of the six Palaearctic species in Tibesti have also been found in the Sahara between the Atlas Mountains and In-Salah (= Ain-Salah), more than halfway Ahaggar, mainly in river beds and oases (Rothschild, 1913). These species have also been found in the northern part of Rio de Oro (Bernardi, 1966). One of them, *Pontia glauconome*, is actually an eremic species. It is obvious that a more humid period can easily bring these species across the Sahara and their isolation in the mountains in the Central Sahara (if they are isolated there at all) is not older than about 5000 years (Postglacial Climatic Optimum). This may also count for the fact that they are subspecifically indistinct from specimens from Algeria.

Of the two remaining Palaearctic species in Tibesti, *Vanessa atalanta* is a well-known migrant, as is the cosmopolitan *Vanessa cardui*. It is not impossible that at least the latter species crosses the Sahara regularly in present times.

*Melitaea didyma* appears to be the only species which requires a colder period for

Table 5. Composition of butterfly species in various regions of the Sahara. Data extracted from Rothschild (1913, 1915, 1921), Riley (1934), Bernardi (1962) and Bernardi &amp; Stempffer (1951)

	NW. Sahara	Ahaggar	Aïr	Tibesti	Palaeartic
<i>Papilio machaon</i>	x	x			x
<i>Pieris rapae</i>	x				x
<i>Pontia daplidice</i>	x	x	x	x	x
<i>glaucanome</i>	x	x		x	x
<i>Euchloe ausonia</i>		x			x
<i>falloui</i>	x	x			x
<i>belemia</i>	x				x
<i>Elphinstonia charlonia</i>	x	x		x	x
<i>Colotis calais</i>			x		
<i>phisadia</i>		x	x	x	
<i>chrysonome</i>		x	x	x	
<i>halimede</i>			x	x	
<i>eupompe</i>			x		
<i>liagore</i>			x	x	
<i>evagore</i>	x		x		
<i>aurora</i>			x	x	
<i>evippe</i>				x	
<i>eris</i>				x	
<i>Pinacopteryx eriphia</i>				x	
<i>Calopieris eulimene</i>				x	
<i>Anaphaeis aurota</i>				x	
<i>Nepheronia buqueti</i>			x		
<i>Colias croceus</i>	x			x	x
<i>Catopsilia florella</i>			x	x	
<i>Eurema brigitta</i>			x	x	
<i>Vanessa atalanta</i>				x	x
<i>cardui</i>	x	x	x	x	
<i>Precis oenone</i>				x	
<i>Byblia ilithyia</i>			x		
<i>Melitaea didyma</i>				x	x
<i>deserticola</i>	x				x
<i>Danaus chrysippus</i>	x		x	x	
<i>Ypthima asterope</i>			x		
<i>Virachola livia</i>		x	x		
<i>Iolaus nursei</i>			x		
<i>Apharitis acamas</i>		x			
<i>Anthea crashayi</i>				x	
<i>Cacyreus lingeus</i>				x	
<i>Castalius cretosus</i>			x		
<i>Tarucus theophrastus</i>	x	x			
<i>rosaceus</i>			x		
<i>Lampides boeticus</i>			x		
<i>Chilades eleusis</i>			x		
<i>Azanus ubaldus</i>			x		
<i>Zizeeria knysna</i>	x		x		
<i>Aricia cramera</i>	x				x
<i>Lycaena phlaeas</i>	x				x
<i>Gegenes nostradamus</i>	x				x



extending its range so far to the south (the mention of this species from the Sahara between the Atlas and Ahaggar by Rothschild, 1913, concerns the related species *M. deserticola*, see Higgins, 1941). It is however surprising that this geographically confusingly variable species in Tibesti occurs in a form which is subspecifically indistinct from the Algerian form, thus suggesting a much more recent contact than the seemingly required Last Glacial.

From Ahaggar three Palaearctic species are known that have not been found in Tibesti, viz. *Papilio machaon*, *Euchloe ausonia* and *Euchloe falloui*. Subspecifically they are scarcely or not at all distinct from the Algerian representatives of the respective species, suggesting that they reached the Ahaggar in relatively recent times. As in the case of *Melitaea didyma* in Tibesti we are forced to suppose a more recent range extension than during the Last Glacial. As *P. machaon* and *E. falloui* have actually been found in the NW. Sahara (Rothschild, 1915), they may even now reach the Ahaggar at times. The Postglacial Climatic Optimum must have been favourable for their range extension, though the temperature was higher than at present, as they could follow a route mainly over higher land (500–1000 m) (Fig. 1). In the same way *Euchloe ausonia* and *Melitaea didyma* may have reached the Central Saharan mountains, though for them the passage was more difficult and their occurrence so far to the south appears the result of a chance colonization.

There are no traces of a penetration from NW. Africa still further across the Sahara. About 400 km south-east of Tibesti extends the Ennedi mountain range. No Palaearctic species are known from this area, except the eremic *Pontia glauconome* (Bernardi, 1964).

Although the Aïr mountains are much closer to Ahaggar than Tibesti, they have only a single Palaearctic species, viz. *Pontia daplidice*. This paucity may be attributed to their much smaller extent and less elevation. It is noticeable that there are no traces left of butterflies colonizing the Central Saharan mountains during the Last Glacial. If they ever did, they died out entirely.

While in the Saharan mountains the affinities with the Palaearctic Region are at the species and even subspecies level, the picture in East Africa is quite different. Of the 25 species in the Ethiopian Region thought to be ultimately of Palaearctic origin (Table 2), less than half (11) are considered specifically indistinct from Palaearctic species and only four or five of them are regarded subspecifically identical. This suggests that the contact with East Africa is at least partly of a much older date, and the various grades of relationship between the Ethiopian and Palaearctic members (subspecific, specific, superspecific, generic) indicate a repeatedly broken contact.

The generally older age of the Palaearctic-E. African contact is due to the fact that only few of the species concerned could use this eastern traverse across the eremic regions during the humid Neolithic, viz. *Pontia daplidice* and *glauconome*, *Euchloe belemia* and *falloui*, *Colias erate* and *Tarucus balkanicus*. Except the last one, these species have also been supposed to have extended their range southward during the same period through the western traverse. Their slight differentiation in the Ethiopian Region is apparently due to the rather recent date of their isolation.

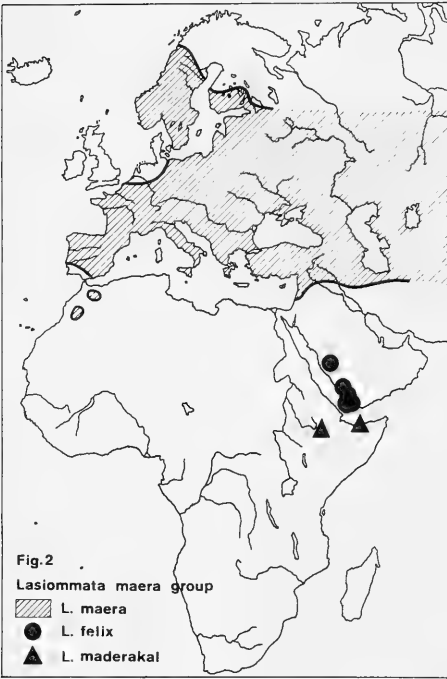


Fig. 2—5. Butterfly species with Palaearctic ancestry in the Ethiopian Region

As the other species need a lower temperature, their isolation must date back at least as far as the last phase of the Last Glacial, i.e. 18,000—25,000 years ago. The differentiation of the *Lycaena phlaeas* group can only be attributed to at least two subsequent southward movements, the first of which (giving rise to *L. orus/clarki*) may also have brought *Pontia helice* to S. Africa. It is impossible to date these movements more or less exactly, but there is no reason to consider them otherwise than coinciding with various phases of the Last Glacial or with an earlier Glacial. The systematic isolation of the *Issoria hanningtoni* group may also be due to a long geographic isolation, from before the Last Glacial.

The history of *Pontia distorta* is still obscure. It is confined to the dry savanna of Somalia and Kenya and may have come there during a dry period across the Ethiopian mountains, but before further suggestions are made, it is advisable to clear up the relationship of *distorta* to other *Pontia* species.

A glance at Fig. 1 shows that in the eastern traverse two routes were available for the temperate species (i.e. the species which needed a cold period for their southward movement), viz. east and west of the Red Sea. The eastern route with its large mountainous areas seems to offer the best opportunities, though using this route the species had to jump the southern end of the Red Sea and a lowland area. From the species known to occur in the SW. Arabian mountains it is clear that many species used this route indeed and it seems possible that most Palaearctic species which reached Ethiopia, did so by way of this route. For species that needed a humid rather than a cold period for range extension the jump over the southern end of the Red Sea must have been still easier.

In table 2 are indicated the species of Palaearctic origin occurring in SW. Arabia. The data are extracted from Gabriel (1954), who mentioned 18 Palaearctic species in SW. Arabia, but he did not mean to state a geographic origin, only to indicate that the species concerned also occurred in the Palaearctic Region. Two of the species listed in table 2 belong to genera which are unrepresented in Africa south of the Sahara (*Eumenis*, *Carcharodus*). Apparently, it was too difficult for these species to make the jump to the Ethiopian highlands (or they became extinct there). The other species are represented by closely related species (*Pararge felix*), or subspecies (*Melitaea abyssinica*, *Lycaena phlaeas*) or by identical subspecies (remaining species) in Ethiopia. These data strongly suggest, that the gap between the SW. Arabian and Ethiopian mountains was not insurmountable for many Palaearctic species (see also the next paragraph and Chapter 5, the paragraph on the Red Sea). Of the Palaearctic species in East Africa only *Pieris brassicoides* and the *Issoria hanningtoni* group have no relatives in SW. Arabia, so that it is quite impossible to say which route they used to reach Ethiopia.

**Summary and conclusions.** Two traverses have been available for a southward movement across the Saharo-Arabian desert zone, viz. a western traverse, from the Atlas Mountains across the W. Sahara and the mountains of the C. Sahara, and an eastern traverse, at either side of the Red Sea. During the cold Glacial Periods and phases, the last of which reached its maximum only 18,000—25,000 years ago,

temperate species could extend their ranges southward through the mountains of the western and eastern traverses, but only traces of a repeated use of the eastern traverse have been left. The western traverse was a dead-end road as there was no link with an Ethiopian mountain range that could support temperate species during warmer times. Even in the C. Saharan mountains no traces are left of glacial range extensions by butterflies from the north.

The very low number of glacial invaders in East Africa and SW. Arabia (about eight) can have various causes:

a. there has been no continuous passage for temperate species, but the passage served as a filter or even the SW. Arabian and E. African mountains were reached by chance colonization;

b. many species which actually reached SW. Arabia/E. Africa, died out during hotter and possibly drier times;

c. many species were in principle well able to make the traverse, but their foodplants failed to do so or at least to establish themselves permanently in SW. Arabia/E. Africa;

d. many species could not compete with Ethiopian species already living in the more temperate habitats.

It seems to me that the main cause for the low number of glacial invaders is a combination of the first two (maybe three) mentioned. This combination was apparently still more effective in the C. Saharan mountains, where glacial invaders appear to be absent at present.

It would be interesting to know the foodplants of all Palaearctic species in the Ethiopian Region. For the *Lycaena phlaeas* group *Rumex* species have been recorded as foodplants and the *Issoria hanningtoni* group is said to live on *Viola* species. As both plant genera are presumably Palaearctic intruders it is unlikely that the butterflies living on it experienced much competition on the part of the Ethiopian species. This may explain their relative success in the Ethiopian Region.

Butterflies capable of living under higher temperatures could move southward during humid periods, the last of which occurred only about 5000 years ago. This relatively recent contact is reflected by the fact that they are slightly or not at all differentiated in their present C. Saharan and E. African habitats. They were not especially dependent on the mountainous traverses of the more temperate species, but as according to Moreau (1966) the eastern Sahara has always been drier than the western part, we may also speak here of a western and an eastern traverse, keeping in mind that the western traverse did not only comprise the mountainous regions, while the eastern traverse may also have included the Nile Valley.

Also for these species the western traverse was a dead-end road. Although the southward penetration has left various traces in the C. Saharan mountains, all species which ever reached the Ethiopian Region by this way have become extinct there. It is even questionable whether these species were ever able to establish themselves well in the probably rather saturated W. African savanna fauna. This can, however, not be the only reason for their absence in W. Africa as some of these species could establish themselves firmly in E. Africa. Apparently the mountains of E. Africa offer better opportunities for survival of these species too, than the possibly too hot, low-lying steppe and savanna along the southern edge of

the Sahara in W. Africa. Also the sudden disappearance of the Mediterranean vegetation from W. Africa shortly after the Postglacial Climatic Optimum (see Moreau, 1966) may have played a part in the absence of Mediterranean butterflies in W. Africa or at least there may be a common cause.

Also the Palaearctic species capable of living in steppe and savanna environments number very low in E. Africa and SW. Arabia (about six) and in this case again, the cause for the low number may have to be looked for in a combination of desiccation and disappearance of foodplants, assuming that there have ever been more species penetrating so far to the south.

In sum, a southward movement of Palaearctic butterflies across the Saharo-Arabian desert zone has occurred various times during the Pleistocene, but penetration into the Ethiopian Region has only been successful (i.e. with still living progeny) through the eastern traverse, along either side of the Red Sea. The effectiveness of the Red Sea itself, especially at its southern end, as a barrier will be dealt with in Chapter 5.

### The northward traverse

For Ethiopian species the Glacial Periods have probably been too cold for a successful northward expansion and a movement in that direction must generally have been confined to periods which were more humid and possibly also warmer than the present one. The last of such periods, the Postglacial Climatic Optimum, occurred only about 5000 years ago and it is to be expected that species, taking this opportunity, have differentiated in the Palaearctic Region very little or not at all. Indeed, eight of the thirteen species of table 3 are not subspecifically distinct in the Palaearctic Region from their Ethiopian representatives and thus, for these species a northward expansion during the Neolithic comes into consideration. Migratory species (*Catopsilia florella*, *Danaus chrysippus*) may have reached the Palaearctic still more recently; *C. florella* is known from the Canary Islands only since about ten years.

If the Palaearctic representative is subspecifically distinct from the Ethiopian stock, this does not mean a priori that the isolation is of an older age. It is quite well possible that *Colotis evagore* developed its Palaearctic race, *nouna*, during the last 5000 years. However, for the two other species concerned, viz. *Charaxes jasius* and *Borbo borbonica*, the situation is somewhat different as they occur discontinuously in the same subspecific form in the West as well as in the East Mediterranean. The absence of differentiation in this area suggests that the distribution has been continuous up to a rather recent time or that there has been a rather recent range expansion within the Mediterranean area. If an Ethiopian species succeeded in expanding its range northward throughout most of the Mediterranean, it is improbable that during a subsequent isolation the Mediterranean range would remain continuous, and thus the development of a single Mediterranean subspecies is improbable. As a consequence, *Charaxes jasius* and *Borbo borbonica* probably became isolated (and differentiated) in the Mediterranean before the Neolithic and extended their range in this area during this humid period.

The two Palaearctic *Spialia* species, *sertorius* and *orbifer*, are specifically distinct from their Ethiopian relatives. They are believed to have originated from a common Ethiopian stock, of which the Ethiopian *mafa* and the Oriental *galba* constitute the remainder of the progeny. As the geographic variation of *sertorius* and *orbifer* reflects the influence of at least the Last Glacial and the origin of *sertorius* and *orbifer* themselves is the result of glacial isolations, the northward expansion of the Ethiopian stock must have occurred earlier. *S. sertorius* and *orbifer* are not restricted to the Mediterranean Region, but can also live under much cooler conditions, while *mafa* ascends at least to 2000 m in the East African mountains. Therefore, it is possible that the northward expansion occurred during one of the earlier Glacial Periods, as a result of the lowering of the montane zone.

As for the southward movement, two routes were available for the northward movement, a western and an eastern one, but the Ethiopian species did not need mountains on their way, only hot and not too dry country. Thus one would expect that during the Postglacial Climatic Optimum many Ethiopian species expanded their ranges northward over a broad front, with the exception of the eastern Sahara, where conditions seem to have always been unfavourable. Nevertheless, at present very few Ethiopian species live in the Palaearctic Region. There is another remarkable feature: almost all Ethiopian penetrations into the Palaearctic Region appear recent, mostly not older than about 5000 years. Only the *Spialia* species indicate a penetration in the early Pleistocene.

The mainly recent arrival of the present Ethiopian species in the Palaearctic Region may be due to the fact that former penetrations (before the Last Glacial) were largely obliterated by the dramatic climatic change during the Last Glacial. The relatively low number of Ethiopian species in the Palaearctic Region at present indicates that postglacially the passage to the north was difficult or that only few species managed to survive till the present day.

An indication of a northward movement over a broad front is found in the present butterfly fauna of the western Sahara and the Saharan mountains. The butterflies must have reached the mountains during a more humid period and they now live there largely isolated, being surrounded by large stretches of uninhabitable land. As they are scarcely, if at all, differentiated from tropical species, the isolation must be recent and as for the Ethiopian species in the Palaearctic Region, the Postglacial Climatic Optimum comes into the picture as a favourable period for northward range extension.

In view of the isolation and rather severe conditions the number of tropical butterflies in the Saharan mountains is not unimportant. Table 6 and Fig. 6 give the numbers and percentages of tropical (i.e. originating from the area south of the Sahara) and non-tropical species in various regions in the Sahara and NW. Africa. As is to be expected, the mountains closest to the southern edge of the Sahara (Aïr, Ennedi) contain the largest percentages of tropical species. Remarkable, however, is the steep decline in the percentage of tropical species in Ahaggar and further to the north, the more so as in northern Rio de Oro, further north than Ahaggar and close to the southern fringe of the Palaearctic Region, the situation is quite different and the ratio tropical-nontropical species is about the same as in Tibesti. As there were ample opportunities for northward range extension only

Table 6. Number of tropical and non-tropical species in various regions in the Sahara and NW. Africa.  
See also Fig. 6

	tropical	non-tropical	total
Morocco-Algeria, N. of Sahara	9	116	125
NW. Sahara	4	13	17
Ahaggar	4	8	12
Northern Rio de Oro <sup>1)</sup>	14	6	20
Tibesti	16	7	23
Air	22	2	24
Ennedi	21	1	22

<sup>1)</sup> only Pieridae

about 5000 years ago, a large-scale extinction of tropical species in Ahaggar and further north during a glacial period cannot be the reason for the present low number of tropical species. In Europe, the Postglacial Climatic Optimum was followed by the cool and wet Sub-Atlantic (2500—2000 BP) (Moreau, 1955). It is unknown how far NW. Africa participated in the decrease of temperature (except that according to Moreau, 1966, a sudden deterioration took place at the end of the Neolithic), but it is well imaginable that a slight drop in temperature would force tropical species living at the edge of their range to withdraw, while near the coast the ocean can have had a tempering effect, so that the drop in temperature was less strongly felt and tropical species could maintain themselves more easily. If we only consider the rapid fluctuations in the ranges of e.g. *Papilio machaon* L., *Araschnia levana* L., *Polygonia c-album* L., in Western Europe during the last

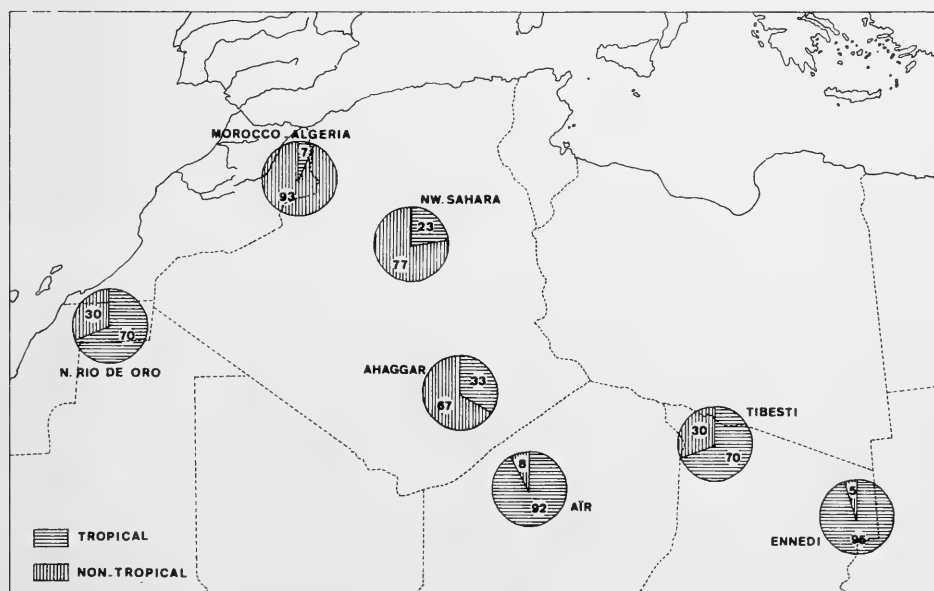


Fig. 6. Composition of butterfly faunas in various regions in northern Africa

century (strongly felt in the Netherlands) which were probably influenced by climatic factors, the above hypothesis is plausible.

Another explanation may be that only few tropical species reached Ahaggar postglacially. According to Moreau (1966) pollen deposits from Tibesti indicate a sudden change in vegetation from Mediterranean to a tropical (Sahelian) one, which was better adapted to drought before the end of the Neolithic. Moreau supposed the Ethiopian plants to have made use of the shores of the expanded Lake Chad (Mega-Chad) that almost reached Tibesti still about 8500 BP, to penetrate as far to the north as Tibesti before the lake was too small and the intervening area too dry. It is understandable that butterfly species following the Sahelian vegetation reached Tibesti (and Aïr?) too late (i.e. it was already too dry) to penetrate still further north.

Thus, the relative poverty of the butterfly fauna of Ahaggar may be due to an extinction of many Palaearctic species, followed by a very limited colonization of Ethiopian species. The fact, however, that only few Ethiopian species live in the Palaearctic part of NW. Africa cannot be entirely due to a limited colonization from the south. The butterfly fauna of northern Rio de Oro shows that the passage through the coastal belt along the Atlantic was easier than across the interior of the Sahara. As this fauna more or less touches the southern fringe of Palaearctic NW. Africa, it appears that the climate of this northern part of Africa is not favourable for Ethiopian species at present, though it may have been in former times. Supposed that a large part of the butterfly fauna of Senegal had ample opportunities to go northwards during the Postglacial Climatic Optimum, the extinction in the north is demonstrated by the following comparison:

In the Niokolo-Koba National Park in SE. Senegal 99 butterfly species have been found (Condamin, 1969) of which 22 are considered relics of a period when the area was better forested, and one (*Vanessa cardui*) is strongly migratory. The remaining 76 species are possible invaders of NW. Africa during the Neolithic. In Morocco, however, only five of these species occur (one tropical species in Morocco is not known from SE. Senegal, viz. *Colotis evagore*). Moreover, in northern Rio de Oro more tropical species of Pieridae have been found than in Niokolo-Koba National Park (14 against 13) and seven of them are not known from the latter area. This suggests a still larger extinction in NW. Africa than indicated by the enormous diverging numbers of tropical butterflies in SE. Senegal and Morocco.

The western route (or rather the area through which passage was possible) was delimited to the east by the waters of Mega-Chad (see above) and the dry eastern Sahara (Libyan desert). In the eastern part of the Saharo-Arabian desert zone the main route to the north will have been the Nile Valley. Braestrup (1947) suggested that even today the middle course of the Nile Valley is too cold to be passed by Ethiopian reptiles and amphibians as the mean and mean minimum temperatures are distinctly lower there than at the Mediterranean coast and in northern Sudan. Apart from drought this may also be a limiting factor to the northward expansion of Ethiopian butterflies today. Thus, since before the Last Glacial only the warm and humid Neolithic is considered for a northward expansion in this area. Also the mountainous routes at either side of the Red Sea have been usable for Ethiopian



species only during this period as at other times they were too dry or too cold or both. Moreau (1966) assumed that during the Neolithic an open to wooded savanna vegetation may have existed in the mountains of SW. Arabia, along the elevated southern edge of the peninsula and in SE. Arabia. Probably a savanna-like vegetation extended northwards following the mountains east of the Red Sea. The route through the mountains west of the Red Sea may have been more difficult to pass as especially in the northern part the mountains are low and vegetation may have been very scarce over long stretches.

Although the eastern traverse (east of the C. Sahara) appears to have been at least as well passable for Ethiopian species as the western one, and the low-lying areas of northern Egypt and the coastal areas of the Middle East must have been favourable for many Ethiopian species to survive, the number of Ethiopian species in the E. Mediterranean equals about that in the W. Mediterranean (the seemingly limited importance of the eastern traverse is biased by the exclusion of Indo-Ethiopian species from this consideration; see paragraph on the indirect West-Palaearctic-Ethiopian affinities, p. 203).

Longstaff (1913, 1916) recorded 95 butterfly species from the White Nile district and southern Kordofan, i.e. from the area fringing the southern edge of the Sahara. The greater part of these species must have been able to go north when the climate improved (became more humid). Nevertheless, only about one quarter of this number (including the species with Indo-Ethiopian distribution) now lives in the E. Mediterranean. Further, Gabriel (1954) listed 97 species of butterflies from SW. Arabia. Excluding the Palaearctic intruders (13), only 20 species (including Indo-Ethiopian ones), i.e. less than one quarter, are also known from the E. Mediterranean.

These facts can lead to one conclusion only: a large extinction of Ethiopian species has taken place in the Middle East during the last 5000 years. It is interesting to note that Moreau (1966) supposed the bird fauna of lower Egypt to have been much richer in species 5000 BP than at present. Apart from proceeding cooling and desiccation, human interference may have played a part in this faunal impoverishment. It appears that Ethiopian species have an extinction rate quite different from Indo-Ethiopian species, see p. 203.

**Summary and conclusions.** Northward range extension across the Saharo-Arabian desert zone has been possible only during more humid and warmer, or at least not colder, periods than the present one. The last of such periods occurred only about 5000 BP (Postglacial Climatic Optimum). Various traces have been left of a northward movement during this period, but there are indications that the Ethiopian species now living in the Palaearctic are only relics of a much richer Ethiopian fauna that became largely extinct in the Mediterranean only during the last 5000 years by cooling, desiccation and human interference.

Similar northward invasions and subsequent extinctions must have taken place during interglacial periods, but only a single relic from before the Last Glacial has maintained itself up to the present day, viz. *Spialia sertorius/orbifer*. Evidently

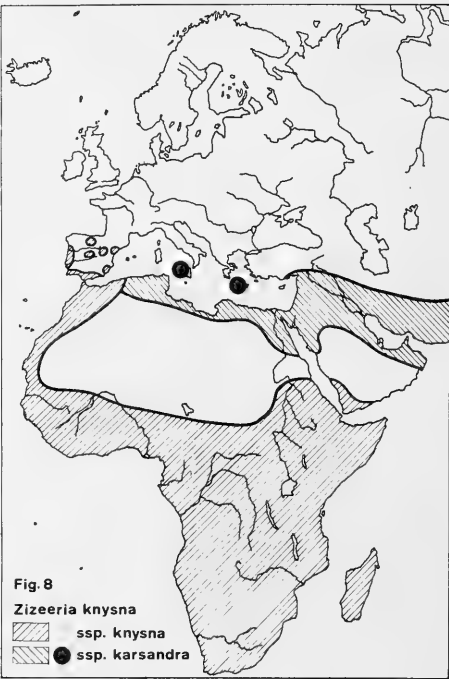
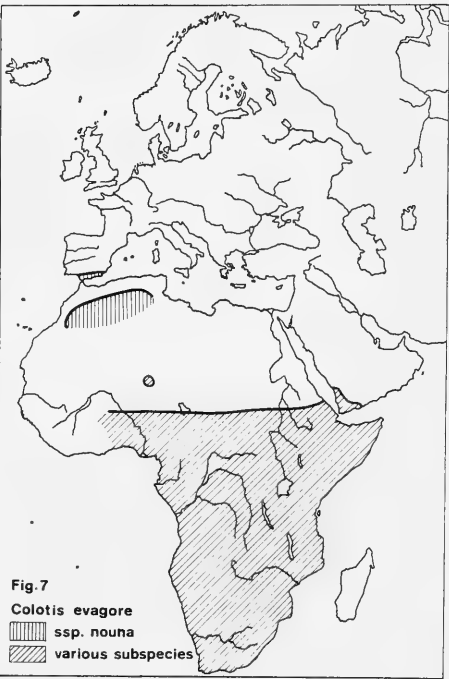


Fig. 7—10. Butterfly species with Ethiopian ancestry in the Palearctic Region

the fact that this relic adapted itself to temperate climates has contributed much to its survival.

As for the southward movement, two traverses were possible, separated by the dry Libyan desert. The western route was situated across the entire western Sahara, but most species expanding northwards through the interior of the Sahara could not get further in time, before the desiccation became disastrous, than the Saharan mountains, where they now live as relics. Ahaggar was already too far to the north for many species. The shorter route through the coastal belt along the Atlantic appears to have been open much longer and to have been the main corridor to the north in this part of Africa. The importance of this corridor is indicated by the large number of tropical Pieridae in northern Rio de Oro. In Palaearctic NW. Africa only very few traces are found of the Neolithic connection. The reason is probably twofold: (a) many species could not establish themselves in the mountainous area of NW. Africa, and (b) most tropical species became extinct in NW. Africa during the last 5000 years.

In the east two routes, now impassable for most species, were open during the Neolithic, viz. the Nile Valley and the mountainous area east of the Red Sea. Their relative importance will be dealt with in Chapter 5. Comparison of the E. Mediterranean butterfly fauna with that of areas near the southern edge of the Saharo-Arabian desert suggests a high extinction rate of tropical species in the E. Mediterranean during the last 5000 years.

For Ethiopian species the eastern and western traverses were almost equally important as far as can be judged from the large numbers of species which possibly used these routes and the small numbers still alive in the W. and E. Mediterranean. As, however, Indo-Ethiopian species also used the eastern traverse, it was much "busier" than the western one.

### The indirect West Palaearctic - Ethiopian affinities

#### The Indo-Ethiopian species

The affinities between the Indian and Ethiopian faunas fall outside the scope of this paper, but some of the species common to both regions also occur in the Palaearctic Region and for that reason they come into the scope of the present study. Moreover, they give supplementary evidence of the importance of the eastern traverse (the western traverse does not come, of course, into consideration).

As for the Ethiopian species, only warm and humid periods can have made possible the faunal contact between the Indian and Ethiopian Regions. We are mainly interested in the last of such periods, the Postglacial Climatic Optimum during the Neolithic, as only common species are involved here and as a consequence of the devastating effect of the Last Glacial it seems improbable that an earlier contact (before the Last Glacial) would be still traceable in the Palaearctic Region.

In our treatment of the northward movement through the eastern traverse by Ethiopian species we already mentioned a difference in the (supposed) extinction

rate between Ethiopian and Indo-Ethiopian species in the E. Mediterranean. This difference is, indeed, remarkable. Of the 74 Ethiopian species recorded by Longstaff (1913, 1916) from the White Nile district and Kordofan, which are possible invaders in the Palaearctic Region, only three (i.e. 4%) occur in the E. Mediterranean, but of the 18 Indo-Ethiopian species ten (56%) have been found in the E. Mediterranean. Similar figures are found by analysing the SW. Arabian butterfly fauna (cf. Gabriel, 1954). Of the 65 Ethiopian species and possible invaders in the Palaearctic Region, only four (6%) are known from the E. Mediterranean, but of the 18 Indo-Ethiopian species 13 (72%) occur in that area.

These obvious differences may have two reasons, viz. (a) real different extinction rate, and (b) different use of the eastern corridor. These two reasons are closely related and probably both played a part. If the Indo-Ethiopian species had a better chance to survive, it would mean that they were better adapted to a dry climate or were more eclectic, capable of living in more diverse habitats, than purely Ethiopian species. This would, at the same time, imply that the eastern corridor was longer passable for Indo-Ethiopian species. Their ability of living in diverse habitats is illustrated by the fact that many Indo-Ethiopian species are migratory (cf. Table 4). It may be more realistic to state that the most adaptable species had the best chance for getting an Indo-Ethiopian range, as undoubtedly their adaptability has contributed to the large extent of their range.

In the Palaearctic, the Indo-Ethiopian species are mainly found in the E. Mediterranean, though in Africa they usually occur as far west as W. Africa. As most of the Indo-Ethiopian species, which are lacking in the W. Mediterranean, do occur in the C. Saharan mountains or even northern Rio de Oro (e.g. *Colotis phisadia*, *Anaphaeis aurota*, *Catopsilia florella*), it appears that their absence from the W. Mediterranean is due to extinction (see paragraph on the northward traverse, p. 197).

### The eremic species

It is impossible to draw a sharp dividing-line between the eremic and Indo-Ethiopian species. To obtain at least a slight idea of the group we may consider the species of Table 4, minus those which are also distributed in Africa south of the equator.

Of some eremic species we can be fairly certain about their geographic origin, e.g. *Pontia glauconome* and *Gegenes nostrodamus*. Such species have been incorporated in the appropriate tables and not in Table 4. The geographic origin of other eremic species is quite uncertain, they have lived so long in the eremic zone that their relationship has become obscure. The Lycaenid genus *Apharitis* is an example of a totally eremic genus. Such species and genera do not belong to the Palaearctic or the Ethiopian fauna and this being so, they are not interesting for the present study. They are the best indication that the barrier between the Palaearctic and Ethiopian Regions is a biome and not a line.

Apart from that it is obvious that their geographic history is closely connected to the alternation of dry and wet periods, and for that reason their distribution and possible geographic variation may indicate possible corridors for faunal exchange

across the eremic zone. However, the number of eremic butterflies is too small for this purpose.

### Remaining genera

As said above (Chapter 3, p. 185) the history of the genera *Papilio*, *Neptis*, *Vanessa*, *Libythea* and *Cyclyrius* is obscure, so far Euro-Ethiopian affinities are concerned. This does not mean a priori that these genera did not make use of the Pleistocene corridors, but in view of the rather remote relationship between the European and Ethiopian members of these genera, a recent traverse is very improbable. Moreover, the European members of the genera (with the exception of the anomalous *Cyclyrius*) also occur in East Asia and it is not impossible that most of them have an East Asiatic origin and invaded the West Palaearctic in rather recent times.

An indication of a Pleistocene Indo-Ethiopian contact is found in the Ethiopian *Papilio demodocus*, which also occurs in SW. Arabia, while the closely related Oriental *P. demoleus* extends from E. Arabia eastward. In the other genera such a recent contact is not demonstrable (with the possible exception of the migratory *Vanessa cardui*).

## 5. BARRIERS OUTSIDE THE DESERT ZONE

The Saharo-Arabian desert zone separates the Palaearctic and Ethiopian Regions, but there are more barriers to a north-south exchange, viz. the Mediterranean and the Red Sea, as Africa today is only connected to other continents by the narrow isthmus of Suez. As this appears to have been also the sole land connection during the whole of the Pleistocene, and it is improbable that all exchange took place across this connection, the effectiveness of the water gaps of the West Mediterranean and the southern Red Sea as a barrier is examined in this chapter.

### The West Mediterranean

As said above (Chapter 4, p. 186) various land connections are thought to have existed during the Tertiary across the West Mediterranean. Thus, at some time before the Pleistocene, the butterfly faunas of NW. Africa and the northern part of the West Mediterranean area must have borne a great resemblance. If we suppose that the present gap of water forms an insurmountable barrier for butterflies, the similarity of the butterfly faunas north and south of the gap must be based on this Tertiary contact. It is very questionable whether a contact broken since then would still be discernible at the species level (indicated by the presence of the same species north and south of the present gap).

A more recent landbridge appears to have existed during the Pliocene in the Tunisia-Sicily area. Therefore, one would expect that the butterflies of NW. Africa bear a greater resemblance to those of Sicily than to those of Spain. This is evidently not true, on the contrary, NW. Africa has more species in common with

Spain than with Sicily. On the other hand, a somewhat greater part of the Sicilian than of the Spanish species is represented in NW. Africa. The differences are undoubtedly influenced by the fact that Sicily is much smaller and with a more limited variety of habitats than Spain. To compensate for this, also the butterfly faunas of Andalusia (for a comparison with Sicily) and of peninsular Italy (for a comparison with Spain) have been considered, while the species which are restricted in Spain to the Pyrenees and Cantabrian Mountains have been left out of consideration. The results are represented in Table 7 (the data are extracted

Table 7. Number of butterfly species in various areas (diagonally), number of species shared by pairs of areas, and (in italics) a faunal similarity coefficient for pairs of areas (see text)

	NW. Africa	Andalusia	Sicily	Spain	Sicily & penins. Italy
NW. Africa	125	91	64	93	74
Andalusia	<i>0.552</i>	131	79	131	94
Sicily	<i>0.395</i>	<i>0.516</i>	101	94	101
Spain	<i>0.431</i>	—	<i>0.492</i>	184	131
Sicily & penins. Italy	<i>0.368</i>	<i>0.503</i>	—	<i>0.645</i>	150

from Higgins & Riley, 1970, and Gomez Bustillo & Rubio, 1974). A similarity coefficient has been calculated from the formula FS (faunal similarity) =

$\frac{(a,b)}{a+b+(a,b)}$ , where a and b are the numbers of species restricted to the regions A and B, respectively, and (a,b) is the number of species common to A and B. This formula allows a quick comparison of resemblances between pairs of regions, though it may be less convenient for further statistical processing.

It appears that the resemblance between the NW. African and Andalusian butterfly faunas is noticeably greater than between the NW. African and Sicilian butterfly faunas. Less noticeable, though still obvious, is the difference between the resemblances of the NW. African-Spanish, respectively the NW. African-Italian butterfly faunas. As the areas Andalusia and Sicily, and also Spain and Italy are more or less comparable in variety of habitats, the above figures suggest that the contact between NW. Africa and Spain has been more intensive or of a more recent date than between NW. Africa and Sicily/Italy, or that the latter area has been subjected to a large-scale extinction of butterfly species which also occur in NW. Africa. For the latter possibility there are no indications at all.

In the above considerations, the direction of the interchange between NW. Africa and Europe has not been taken into account. Of the 125 NW. African butterfly species, 83 can with reasonable certainty be considered northern invaders, the remaining 42 species invaded NW. Africa from the south or east, or we cannot be certain about their geographic origin. Of the 83 supposedly northern species, 14 do not occur in Spain or Italy; they are mainly endemic species which are regarded closely related to European species; further, 67 are also known from Spain and 54 from Italy (incl. Sicily). These numbers are almost the same percentages of the total number of butterflies in the respective regions (Spain

36.4%, Italy 36%), and therefore, it would seem unlikely that either of these two regions contributed more (in relation to its own fauna) to the population of NW. Africa. We can, however, analyse the data further. There are 49 species in Spain (excl. Pyrenees and Cantabrian Mountains) which are lacking in peninsular Italy (and Sicily); of these, 15 (30.6%) occur in NW. Africa. On the other hand, 15 species occurring in peninsular Italy and Sicily are absent in Spain, and of these only two (12.5%) (*Hipparchia aristaeus* Bonelli, and *Satyrus ferula* Fabr.; the latter also occurs in the Spanish Pyrenees) are found in NW. Africa. This again points strongly to the assumption that the connection across the Straits of Gibraltar has been of greater importance to the present relationship between the NW. African and European butterfly faunas than the Sicilo-Tunisian corridor.

The number of species which came from NW. Africa is very small. Indeed, only four species can be listed as such, viz. *Colotis evagore*, *Tarucus theophrastus*, *Zizeeria knysna* and *Borbo borbonica*. All occur in Spain, but only the second and third are known from Sicily and peninsular Italy. Consequently, also for the northward exchange the Gibraltar corridor appears to have been most important for the present situation. It is interesting to note here that *Z. knysna* evidently used the Gibraltar as well as the Sicilo-Tunisian corridor, as the Moroccan *Z. knysna knysna* occurs in Spain and the Algerian *Z. knysna karsandra* in Sicily.

Further indications of the importance of the Gibraltar corridor are found in the geographic variation. The excessive splitting performed in most butterflies with regard to their subspecies is a serious hindrance to this kind of examination and for that reason I have extracted the figures given below from Higgins & Riley (1970), who have lumped subspecies to a large extent, with some additional information.

Of the 39 species which occur in NW. Africa, Spain, Sicily and peninsular Italy, and of which at least two subspecies are recognized, seven occur with the same subspecies in all these regions, four with a different subspecies in each region, 17 with the same subspecies in Spain and Italy, but distinct in NW. Africa, three with the same subspecies in NW. Africa but distinct in Spain, and eight with the same subspecies in NW. Africa and Spain, but distinct in Italy. An interesting case is found in *Carcharodus alceae*, which shows two genitalic forms, one restricted to NW. Africa and S. Spain-S. Portugal, the other from S. Spain throughout the remainder of the range of the species, including Italy (De Jong, 1974a).

**Conclusion.** All observations point to a more recent and more intensive contact between NW. Africa and Europe through the Gibraltar corridor than through the Sicilo-Tunisian corridor. As the Sicilo-Tunisian landbridge was the last terrestrial connection in this area and was severed in the Pliocene, it follows that much or most of the contact took place across the water gap of the Straits of Gibraltar and not through a landbridge. The great resemblance, even subspecific, between the NW. African and Spanish butterfly faunas suggests a regular Pleistocene contact. Apparently, the influence of Tertiary landbridges in the Gibraltar or Sicilian area has been largely overwhelmed by later contacts. The fact that only a rather arbitrary part of the European butterfly fauna succeeded in colonizing NW. Africa

is undoubtedly the result of the filtering effect of the Gibraltar water gap. The Sicilian corridor was apparently much more difficult to pass in the Pleistocene and few species have crossed this large sea gap.

In sum, at least in its western part the Mediterranean has not acted as an insurmountable barrier for north-south exchange, and consequently, its influence on the faunal exchange between the Palaearctic and Ethiopian Regions has been small.

### The southern Red Sea

The area between the Red Sea and the Nile is much less elevated than the area east of the Red Sea (see Fig. 1). West of the Red Sea, between northern Egypt and Eritrea, elevations over 1000 m are only found on a series of isolated mountains close to the Red Sea, but east of the Red Sea elevations over 1000 m occur continuously from the Middle East to Yemen. Therefore, the latter area appears to have been most convenient for temperate Palaearctic species to go south. However, such species ran up against the water gap of the Red Sea in their southward expansion, as the Red Sea opened before the Pleistocene. According to Moreau (1966) the width of the Red Sea would have been little affected by the lowering of the ocean level during the glaciations, but as the maximum lowering of the ocean level amounted to at least 100 and probably 200 m, the width of the southern part of the Red Sea must have been influenced largely and a lowering of 200 m must have connected Eritrea to SW. Arabia.

Apart from the Red Sea the temperate Palaearctic species had to cross low-lying grounds to reach the Ethiopian mountains. There is no reason to suppose that at any time during the Pleistocene the habitats of these species were distributed continuously from the Middle East to East Africa. It is, therefore, not surprising that but few temperate Palaearctic species succeeded in colonizing the African mountains. But the present question concerns the effectiveness of the southern Red Sea as a barrier. For some species (cf. Table 2) the Red Sea has been insurmountable, indeed: for the *Hipparchia* stock which gave rise to *H. tewfikii*, and for *Tarucus balkanicus* and *Carcharodus alceae*, the route east of the Red Sea has apparently been a dead-end road, as they did not reach Ethiopia. Other species clearly show that the jump from SW. Arabia to the mountains of Ethiopia has been possible, as they (or one of their subspecies) are (mainly) restricted to SW. Arabia and Ethiopia. They are: *Melitaea abyssinica*, the vicariant species *Lasiommata maderakal* and *felix*, the vicariant subspecies *Lycaena phlaeas pseudophlaeas* and *phlaeas shima*, and *Spialia doris doris*. For the other species of Table 2 a contact across the Red Sea is not needed to explain their present distribution, as they may have gone southward by a route west or west as well as east of the Red Sea. In some cases, especially *Pieris brassicoides*, *Pontia helice* and the *Issoria hanningtoni* group, it is also feasible that they migrated south through the Arabian mountains, traversed the Red Sea, penetrated the East African mountains and became extinct in SW. Arabia. Other species, less dependent on the cooler climate of the mountains, may have gone southward west of the Red Sea or even through the Nile Valley. I agree with Larsen (in litt.) that the present occurrence of *Gegenes*



*nostradamus* along the Nile southward is of a recent date and has to do with the preference of the species for oasis environments. Similar instances may be found in other species as well.

In sum, for Palaearctic species the southern end of the Red Sea has acted as a filter which was probably passed by the majority of the species. This filter has been important for the north-south exchange, as probably most Palaearctic species to go south used the route east of the Red Sea.

For the Ethiopian species which expanded their ranges to the north, the Red Sea did not form a barrier as they could use the route west of the Red Sea and the Nile Valley. Nevertheless, many species crossed the Red Sea and it possibly was the main route for Indo-Ethiopian species. Gabriel (1954) listed 97 *Rhopalocera* from SW. Arabia, of which 86 are also known from Ethiopia and/or Somalia. If we extract the eight Palaearctic species, 78 tropical species once must have crossed the Red Sea. This number appears large if compared with the about 420 species of *Rhopalocera* known from Ethiopia (Carpenter, 1935; Gabriel, 1949), but if we consider that Ethiopia is very much larger and has a much greater variety of habitats, it is clear that the crossing of the Red Sea has not given much difficulties for many tropical species. It is unknown whether they could make use of a possible glaciâ land connection or had to jump the water gap during warmer times. At any rate, the crossings have been possible to a recent date, as only 12 of the tropical species in SW. Arabia occur in a subspecific form distinct from the form in Ethiopia. The Tertiary contact before the Red Sea opened at its southern end is not traceable in the present butterfly fauna of SW. Arabia, i.e., such contacts have been swept away by later invasions.

**Conclusion.** During the Pleistocene the southern end of the Red Sea has been a filter for exchange between Arabia and Ethiopia, but it did not act as a strong barrier, as probably more species passed through than were stopped. The filter effect was performed by the water gap of the Red Sea and for part of the species by the low-lying area between the Red Sea and the Ethiopian highland. During maximum glaciation a landbridge may have existed between SW. Arabia and Ethiopia, but the assumption of such a landbridge is not essential for the explanation of the present distributions.

## 6. SUMMARY AND CONCLUSIONS

1. The Saharo-Arabian desert zone has not always hampered the faunal exchange between the West Palaearctic and Ethiopian Regions to the same extent as today. To the contrary, movements across this zone have not been very rare, though survival in the newly won area up to the present day is a rare event.

2. Affinity between the West Palaearctic and Ethiopian Regions at the genus level, without common species or superspecies, may date back to Tertiary times, but does not necessarily do so. In these cases it is often difficult to decide whether the affinity is a result of direct exchange or that one of the regions received the congeneric species from some source outside the other region.

3. The occurrence of a species or superspecies north as well as south of the desert zone is supposed to be the result of a Pleistocene contact across this zone.

4. During the last phase of the Last Glacial Period (Kenya Glacial = last maximum of Würm Glacial), only 12,500-25,000 BP, the temperature decreased to 6°C lower than today in East Africa. This rendered the montane zone in East Africa, the lower limit of which is at 1500 m at present, the possibility to descend to 500 m. Such a lowering of the montane zone facilitated the traverse across the Saharo-Arabian desert zone through mountain ranges by temperate species. Similar conditions must have occurred during earlier Glacial Periods. These periods were not necessarily more humid than the present one and, apart from this, they were generally too cold for Ethiopian species to extend their ranges northward.

More humid periods also occurred more than once during the Pleistocene, the last one during the Neolithic (Postglacial Climatic Optimum), only 4500-7500 BP. During the Neolithic the temperature was about 2°C higher than today. These conditions were favourable for Ethiopian species to go north, but bad for temperate species to go south as their habitats in the mountains became much more isolated and the lowland was too hot. Only Mediterranean species may have been able to move southward. The Ethiopian species were not dependent on mountain ranges, as at least in the western Sahara the warm lowland was also clothed with Mediterranean vegetation. The eastern Sahara appears to have always been dry. The present bare condition of the western Sahara is young and does not date back further than 4500 BP, but similar dry conditions have existed earlier in the Pleistocene.

5. As the Palaearctic species were largely dependent on mountainous areas for their southward expansion, two routes were available, viz. at either side of the Red Sea and from the Atlas Mountains across the mountains in the Central Sahara. The latter (western) route was a dead-end road as it did not lead to a mountain area in the Ethiopian Region, where the Palaearctic species could survive warmer periods. There are no traces left of a southward expansion through the western route during glacial periods. The occurrence of Palaearctic species in the Central Saharan mountains is supposed to be of a more recent, Neolithic age. The limited importance of the western route was not caused by the Straits of Gibraltar acting as a barrier to the supply of Palaearctic species to the south, as this sea gap was regularly crossed.

The eastern route offered better facilities for Palaearctic species as it led to the mountains of East Africa with ample opportunities for survival during warmer periods. All extant temperate Palaearctic species in the Ethiopian Region used this route, especially through the mountains east of the Red Sea. The southern end of the Red Sea has not acted as an effective barrier on this way. The various degrees of differentiation of the penetrating populations from their Palaearctic ancestors (development of Ethiopian subspecies, species, species groups) indicate a repeated use of the eastern route during the Pleistocene, and the highest degree of differentiation (the *Issoria hanningtoni* group) may be the result of a Late Tertiary invasion.

Mediterranean species (e.g. *Pontia daplidice*, *Euchloe belemia*, *Tarucus balkani-*

*cus*) may have used the Nile Valley and probably also the mountain ranges at either side of the Red Sea to go southward various times during the Pleistocene and for the last time as late as 5000 BP (Neolithic). Probably because their habitat preference largely overlaps that of many Ethiopian species, they never attained an extensive Ethiopian range, while some of the more temperate species eventually reached South Africa and Cameroon. The only exception may be *Gegenes pumilio*.

In view of the opportunities offered and the species available (more than 400 in the West Palaearctic), the number of about 17 successful southward crossings is low. This little success is due to extinction following an initially successful penetration as a result of climatic change (increasing temperature), and perhaps to unknown obstacles on the way, so that not many Palaearctic species ever reached the Ethiopian Region.

6. For the Ethiopian species the Glacial Periods of the Pleistocene were too cold for a penetration into the Palaearctic Region. They only needed a more humid period than the present. The last of such periods, the Neolithic, occurred only about 5000 BP. During the Neolithic a large-scale northward movement through the western Sahara (especially through the coastal regions, but also far inland), the Nile Valley, and probably along the Red Sea took place. Most of the species involved in this movement died out subsequently in the Palaearctic as a result of decreasing temperature, desiccation and human interference. Most relics of the northward penetration are found near the Atlantic coast (northern Rio de Oro), and in the high mountains of the Central Sahara, but Ahaggar was probably too far for most Ethiopian species to be reached before the desiccation became disastrous. Because the isolation of the relics is so young, they are scarcely, if at all, differentiated from their parental Ethiopian stock.

If we suppose that during the Neolithic all possible invaders into the Palaearctic (judged from their present occurrence in the northernmost part of the Ethiopian Region) virtually reached the Palaearctic, we have to consider an extinction rate of Ethiopian species in NW. Africa as well as in the E. Mediterranean, of about 90 % during the last 5000 years.

Humid periods have occurred various times during the Pleistocene, but the resulting northward expansions of Ethiopian species have scarcely left traces, as almost all pre- and interglacial colonizations in the Palaearctic have been swept away by the devastating effect of the glaciations. A notable exception is the common ancestor of the now entirely Palaearctic species *Spialia sertorius* and *orbifer*, which invaded the Mediterranean probably in early Pleistocene times, while two other species (*Charaxes jasius* and *Borbo borbonica*) appear to have gone through at least the last phase of the Würm glacial in the Mediterranean.

The Nile Valley may have been the highway in the eastern part of the Saharo-Arabian desert zone for Ethiopian species bound for the north, but also east of the Red Sea the passage was viable. The gap of the southern end of the Red Sea did not act as an important obstacle on this way.

7. In relation to the total number of butterfly species in the West Palaearctic (more than 400) and Ethiopian (almost 2700) Regions the numbers of successful invasions (i.e. those maintaining themselves up to the present day) (about 17 and

12, respectively) into the other region are small and remarkably different. The difference is due to the fact that the Ethiopian Region offered much more opportunities for survival of Palaearctic species in mountain areas during warmer periods, than the Palaearctic Region for survival of Ethiopian species in lowland areas during colder periods. This also explains why the southward traverses seem to cover a longer period than the northward ones: the species concerned had a better chance to survive.

8. Ecologically more flexible tropical species could attain an Indo-Ethiopian distribution. Several of these species also occur in the West Palaearctic Region. Although it is at present not clear whether the Palaearctic representatives originated from the east or from the south, some may indeed have an Ethiopian origin. Even if we consider all Indo-Ethiopian species in the Palaearctic to be of Ethiopian origin, increasing the number of successful northward crossings to about 20, the relative number of successful crossings is only slightly influenced and the difference with the relative number of successful northward crossings is almost untouched: the difference would only disappear if we could demonstrate more than 100 successful northward crossings.

9. From all considerations above we arrive at the final conclusion:

At present the Saharo-Arabian desert zone separates the Palaearctic and Ethiopian Regions and as a result of the bare condition of this zone faunal exchange is impossible. The desert zone is, however, not the only factor that keeps the Palaearctic and Ethiopian faunas separate. During the last 2 millions of years (the Pleistocene) the desert zone has often been passable in both directions, leading to important faunal exchange, but most penetrating species became extinct as a result of climatic changes. Thus, the Saharo-Arabian region dosed the faunal exchange, and the extinction of colonists subsequently reduced the initial success of the exchange. As both the dosing and the extinction are due to climatic changes and a single climatic change could lead to extensive faunal exchange, we can finally state that the main factor keeping the Palaearctic and Ethiopian faunas apart, at least during the Pleistocene, is the repeated climatic change.

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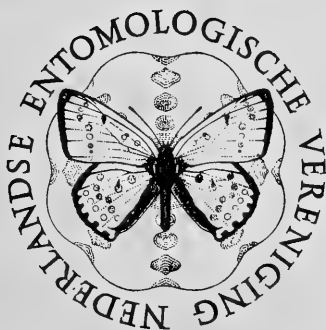
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

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## INHOUD

E. A. LOELIGER. — The enigma of *Celerio hybr. Pauli* Mory, p. 217-219, pl. 1.



# THE ENIGMA OF *CELERIO HYBR. PAULI* MORY

by

E. A. LOELIGER

*Hofdyck 48, Oegstgeest, Netherlands*

With one colour-plate

## INTRODUCTION

In the summer of 1897, the well-known Swiss entomologist M. Paul observed on *Hippophae rhamnoides* in the vicinity of Sion, Wallis, Switzerland, a sphinx caterpillar resembling *Celerio euphorbiae*. Unfortunately, the detailed description of the caterpillar has been lost. Breeding of the caterpillar was successful, however, and on September 1st of the same year the moth emerged. It was put at the disposal of Prof. Standfuss for his collection (Fig. 1; at present kept in the Entomology Institute of the Eidgenössische Technische Hochschule at Zürich, Switzerland). Shortly thereafter, the medical student Mory published a photograph together with a detailed description of the moth. The author, on the basis of a comparative study, thought that it could be the product of a natural cross-breeding of *Celerio euphorbiae* ♂ with *Celerio hippophaes* ♀, since called *Celerio hybr. Pauli* Mory (1901). Several years later, Denso (1911) denied the probability suggested by Mory for two reasons. First, caterpillars from experimentally obtained crossbreeding of *Celerio euphorbiae* ♂ with *Celerio hippophaes* ♀, although clearly resembling those of *Celerio euphorbiae* could only be bred *ab ovo* on *Euphorbia cyparissias* or other *Euphorbia* species. Second, the resulting moths differed in various ways from Paul's specimen. Since it remained possible that the latter was a bastard resulting from a cross between *Celerio livornica* and *Celerio hippophaes*, Denso gave the experimentally obtained bastard of *Celerio euphorbiae* ♂ with *Celerio hippophaes* ♀ the name *Celerio hybr. euphaes* (see Denso, 1911).

Paul's finding remained enigmatic. With the present report we offer a possible solution of the problem of a *Celerio euphorbiae*-like caterpillar to be found on *Hippophae rhamnoides*, a solution which might serve as a model holding equally well for bastards of *Celerio livornica* crosses with *Celerio hippophaes*.

## EXPERIMENT

The materials used for the experiment which gave the desired result were the genuine species *Celerio euphorbiae* and *Celerio hippophaes*, found in the summer of 1973 in the Wallis region of Switzerland. Brought to Holland, the pupae hatched as early as the latter part of 1973, and cross-breeding of *Celerio hippophaes* ♂ with *Celerio euphorbiae* ♀ (*Celerio hybr. hippophorbiae*) under strictly aseptic conditions

was successful on *Euphorbia cyparissias* and/or *polychroma*. In 1974, the following cross-breeding with this hybrid succeeded:

1. *Celerio hybr. hippophorbiae* ♂ × *Celerio hippophaes* ♀, and
2. *Celerio hybr. hippophorbiae* ♂ × *Celerio euphorbiae* ♀.

Caterpillars of variety 1 were highly variable and accepted only *Hippophae rhamnoides*; some of them strongly resembled the caterpillars of *Celerio hippophaes*, but none those of *Celerio euphorbiae*. Variety 2, on the other hand, was very similar to *Celerio euphorbiae*, and accepted only leaves of *Euphorbia cyparissias* and/or *polychroma*. Most of the pupae of both varieties hatched in September of 1974. Probably supported by excellent climatological conditions, cross-breeding of *Celerio hybr. (hippophorbiae × euphorbiae)* ♂ with *Celerio hybr. (hippophorbiae × hippophaes)* ♀ was again successful three times. The three female moths together yielded about 150 fertile eggs. Approximately 25 per cent of the caterpillars accepted *Hippophae rhamnoides* leaves and developed extremely well; the rest did equally well on *Euphorbia polychroma*. Most of these caterpillars resembled another successfully obtained bastard, the result of cross-breeding of *Celerio hybr. (hippophorbiae × hippophaes)* ♂ with *(hippophorbiae × hippophaes)* ♀. However, a far from negligible number of not only the caterpillars raised on *Euphorbia polychroma* but also of those kept on *Hippophae rhamnoides*, were almost indistinguishable from *Celerio hybr. hippophorbiae*, i.e. resembled *Celerio euphorbiae* rather closely so that observers less familiar with the detailed pattern of this *Celerio* species would probably have concluded that these were *Celerio euphorbiae* caterpillars of the red (Fig. 3), or the yellow, or even of the black variety (Fig. 4).

## DISCUSSION

Cross-breeding is rather common in nature (Mory, 1897). Moreover, the two species in question, *Celerio euphorbiae* and *Celerio hippophaes*, live near each other in the foreland of the Rhône River in the Wallis region. In captivity, *Celerio hybr. euphaes* Denso is one of the most easily obtained bastards. *Ab ovo* caterpillars of this crossing, however, do not accept *Hippophae rhamnoides*. Hence, in nature this bastard is doomed to death. However, the reciprocal bastard, *Celerio hippophorbiae* which is obtained just as easily in captivity, grows very well on the fodder plant of the maternal family. Caterpillars of both of these primary bastards produce highly fertile moths. Secondary bastards are therefore easily obtained: whereas the variety *Celerio hybr. hippophorbiae* ♂ × *Celerio hippophaes* ♀ lays the eggs on and accepts *Hippophae rhamnoides*, the reciprocal bastard, *Celerio hybr. hippophorbiae* ♂ × *Celerio euphorbiae* ♀, does the same with the various *Euphorbia* species growing in the Wallis region. Of these two, the rather sophisticated recombination of *Celerio hybr. (hippophorbiae × euphorbiae)* ♂ with *(hippophorbiae × hippophaes)* ♀ in captivity has been shown to lay eggs on *Hippophae rhamnoides*, which is accepted by approximately one-fourth of the emerging caterpillars, even those strongly resembling *Celerio euphorbiae*. This tertiary bastard now might have been responsible for Paul's finding of an *euphorbiae*-like caterpillar on *Hippophae rhamnoides*. The fact that *ab ovo* caterpillars of the two primary bastards *Celerio hybr. euphaes* and *Celerio hybr. hippophorbiae* do not accept *Hippophae rhamnoides*,

whereas the cross *Celerio hybr. (hippophorbiae*  $\times$  *euphorbiae*)  $\delta$  with (*hippophorbiae*  $\times$  *hippophaes*)  $\text{f}$  does so, including *euphorbiae*-like specimens, must be explained by chromosomal crossing over.

Unfortunately, the adults of our tertiary bastards (Fig. 2) are all distinctly different from *Celerio hybr. Pauli* (Fig. 1). We must consequently agree with Denso's criticism and reconsider the possibility of a bastard with another *Celerio* species, most likely with *Celerio livornica*, particularly because of the white flames on the thorax. Such flames were not present on any of the specimens bred by us. If *ab ovo* caterpillars of the primary bastard of *Celerio livornica* and *Celerio hippophaes* too should prove unable to grow on *Hippophae rhamnoides* (which is certainly also the case for *Celerio hybr. vespertilioides* and *Celerio hybr. irene*), our observation would offer a model for further experiments with these two species of the genus *Celerio*, to elucidate the enigma of *Celerio hybr. Pauli* Mory. *Celerio livornica* is a frequent and well-known guest of the Wallis region, coming from the Mediterranean area, and its fodder plants are even more ubiquitous than those of *Celerio euphorbiae*.

#### ACKNOWLEDGEMENT

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#### SUMMARY

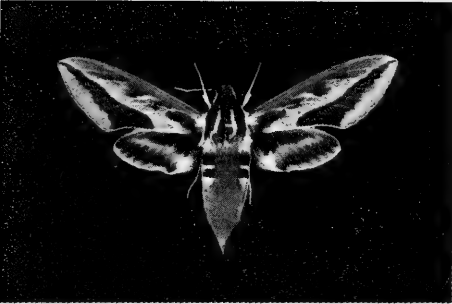
A tertiary bastard was obtained by crossing *Celerio euphorbiae* with *Celerio hippophaes*, i.e. *Celerio hybr. (hippophorbiae*  $\times$  *euphorbiae*)  $\delta$  with (*hippophorbiae*  $\times$  *euphorbiae*)  $\text{f}$ . An appreciable proportion of the *ab ovo* caterpillars of this bastard, many of which clearly resemble those of *Celerio hybr. hippophorbiae* (and hence of *Celerio euphorbiae*), accept *Hippophae rhamnoides*, which for *ab ovo* caterpillars of the primary bastard *Celerio hybr. euphaes* and *Celerio hybr. hippophorbiae* is never the case. Although the emerging moths are distinctly different from *Celerio hybr. Pauli*, our experiments might serve as a model for cross-breeding experiments between *Celerio hippophaes* and other *Celerio* species such as *Celerio livornica*, in order to explain the enigmatic observation made by Paul in 1897.

#### LITERATURE

- Denso, P., 1911. *Celerio hybr. hippophaes*  $\delta$   $\times$  *euphorbiae*  $\text{f}$  und *hybr. euphorbiae*  $\delta$   $\times$  *hippophaes*  $\text{f}$ . — Entomol. Zeitschr. 25: 151—153.
- Mory, E. von, 1901. Ueber einige neue schweizerische Bastarde des Sphingiden-Genus *Deilephila* und die Entdeckung abgeleiteter Hybriden in der Natur, sowie Beschreibung einer neuen Varietät von *Deilephila vespertilio* Esp. — Mitt. Schweiz. entomol. Ges. 10 (1): 333—360.



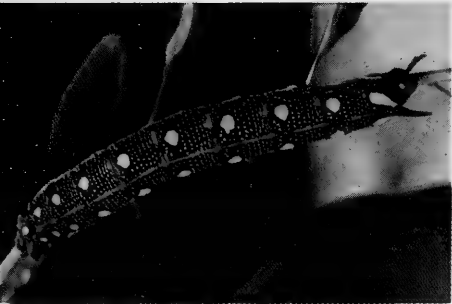




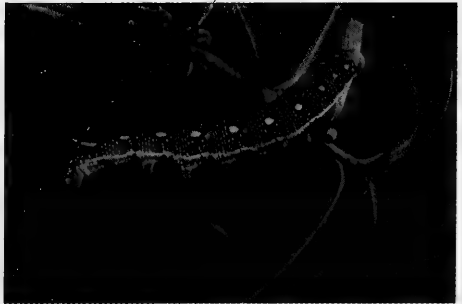
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Fig. 1. *Celerio hybr. Pauli* Mory; original specimen in the Standfuss collection at Zürich (courtesy of Prof. Dr. W. Sauter, director). Fig. 2. Cross-breeding of *C. hybr. (hippophorbiae x euphorbiae)* ♂ × *(hippophorbiae x hippophaes)* ♀, supposed to be *C. hybr. Pauli*. Fig. 3 and 4. Caterpillars of *C. hybr. (hippophorbiae x euphorbiae)* ♂ × *(hippophorbiae x hippophaes)* ♀, supposed to be *C. hybr. Pauli*, red variety on *Euphorbia polychroma* (3) and black variety on *Hippophae rhamnoides* (4), respectively







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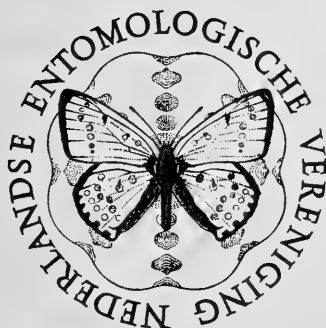
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# AUTUMN FAUNA OF COLLEMBOLA FROM CENTRAL CRETE<sup>1)</sup>

by

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With 46 text-figures

## ABSTRACT

A systematic and faunistic account of the Collembola occurring in central Crete is presented. All material was collected in the second half of October, 1972, by various techniques, including portable Berlese funnels. In all, 93 species are recognized. Of these, 15 represent new taxa: the new species *Mesaphorura critica*, *Onychiurus xenonis*, *Acheroxenylla cretensis*, *Hypogastrura tethyca*, *Xenyllodes minitaurus*, *Pseudachorutes (Pratanurida) mucronata*, *Neanura cretensis*, *Lathriopyga anthrenoidea*, *Cryptopygus triglenus*, *Clavisotoma albertinae*, *Dimorphotoma porcellus*, *Troglopedetes cretensis*, and *Pseudosminella paprivata*, and two new subspecies *Odontella nana orientalis* and *Sminthurinus alpinus bisetosus*. The new genus *Acheroxenylla* (monotypic for *A. cretensis* n. sp.) closely resembles *Xenylla* but has only 2+2 ocelli. *Heteromurus sexoculatus* Brown, 1926, and *Seira graeca* Ellis, 1966, are revalidated. *Onychiurus sublatus* Gisin, 1957, *O. gisini* Haybach, 1960, are synonymized with *O. prolatus* Gisin, 1956, as well as the two subspecies *O. p. conlatus* Gisin, 1962, and *O. p. trilatus* Gisin, 1963. A key is given to recently described species of *Mesaphorura*, and the better-known European *Seira*. Critical discussions of many species are included, and mass occurrences of *Clavisotoma albertinae* and *Dimorphotoma porcellus* are reported.

## INTRODUCTION

Although Crete has received much attention from collectors, its collembolan fauna has been completely neglected. To make a start on the faunistic and systematic exploration of the springtail fauna of this splendid island, the author and his wife made a collecting trip between Oct. 14th and Oct. 30th in 1972. Since we had our base in Iráklion, mainly this region was sampled. This is the lowest, and possibly not the most interesting part of the island, and extensive collecting in the mountains is still urgent. Nevertheless, an interesting fauna was found.

The time of collecting coincided with the transition from the summer drought to the autumn rains; this is the short season when geophytes produce their leaves, and annuals germinate, twining the landscape from brownish-yellow to green within a couple of weeks. All of the collected material is treated here, and all specimens are kept (mostly on slides, mounted separately in Marc André II unless otherwise mentioned) in the collections of the Zoölogisch Museum, Amsterdam.

The material was collected manually, with the sweeping net, or more usually with a set of portable Berlese funnels based on the model advocated by J. T.

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<sup>1)</sup> Manuscript received: 15 August 1975

Salmon. Unless specified otherwise, all collecting sites were at altitudes of less than 400 m above sea-level. To avoid undue length, the list of references is in general restricted to descriptions published since the appearance of Salmon's Index to the Collembola (1964).

This is my third contribution to the study of the Greek fauna (the first, on two species from the mainland, was published as early as 1966, the second, concerning the fauna of Rhodes, appeared in 1974). Since more are planned, zoogeographical and ecological discussions are kept to a minimum in the present paper. These subjects will receive the attention they deserve after the fauna of more localities has been treated.

Again, help without which this paper could not have been completed was generously given by colleagues, among whom special mention should be made of J.-M. Betsch (Brunoy), R. Dallai (Siena), P. N. Lawrence (London), P. F. Bellinger (Northridge, California), Z. Massoud (Brunoy), A. Szeptycki (Kraków), and R. Yosii (Kyoto). The assistance of our technician, L. B. Panday, and our secretaries T. Dovale and E. C. Gräper is gratefully acknowledged. Prof. J. H. Stock and Prof. J. T. Wiebes are sincerely thanked for their critical reading of the manuscript.

#### List of samples

1. Kríti, Thérisos, 14.x.1972, (ca. 5 km W. of Iráklion), upper 5 cm of rather dry, comparatively loose loam covered by *Capparis* spec., on slope along street; author's collection number 972.215.
2. Tsagarák (a village 17 km S of Iráklion, along the Giófiros River), 15.x.1972, crumbly, dry loam, sampled at a depth of 10 cm in an olive grove without undergrowth; 972.217.
3. Tsagarák, litter and topsoil (small hard lumps of dry loam) under an isolated *Quercus coccifera* L. in phrygana (i.e., a very common low vegetation type, comparable to the French garigue, consisting mainly of small shrubs and geophytes); 972.234.
4. Festós, 16.x.1972, rather damp, crumbly loam in trodden meadow on small island in the Geropótamos River; 972.197.
5. Festós, rather dry crumbly loam with many roots and many stones in small bush along Geropótamos, consisting of *Vitis*, *Punica*, and *Ficus* with little undergrowth of geophytes; 972.227.
6. Festós, along Geropótamos: loose soil and root-mat of an opulent vegetation comprising various herbs and tall grasses (ca. 60 cm) with a somewhat ruderal appearance; 972.239.
7. Festós, along Geropótamos; trodden, compact, rather moist loam with many pebbles, under a low vegetation, mainly clover; 972.236.
8. Festós, along Geropótamos: swept from low grass of meadow; 972.213.
9. Fortétssa (about 5 km SE of Iráklion), 18.x.1972, after two days of heavy rain, wet swollen loam of vineyard; 972.224.
10. Fortétssa, wet sandy loam, trodden and ruderal, with some perennial grasses; 972.230.



11. Fortétsa, moist compact loam under large almond tree in fallow field; many goat droppings; 972.208.
12. Ioúchtas, a hill near Archánes, 10 km SSW of Iráklion, 19.x.1972, 620 m, loose warm-brown terra rossa under low bushes in phrygana, west exposition; 972.240.
13. Ioúchtas, 700 m, loose terra rossa half under *Quercus coccifera* on yoke of the hill; 972.221.
14. Ioúchtas, 760 m, loose terra rossa in phrygana on west exposition; 972.229.
15. Ioúchtas, 600-700 m, swept from bushes (mainly *Pistacia lentiscus* L.); 972.210.
16. Amnisós, 5 km E of Iráklion, 20.x.1972, stony yellowish compact loam under *Sarcopoterium* bush in degraded phrygana on weak east slope; 972.238.
17. Amnisós, rather dry, loose, humus-rich sand on 3 m high cliff, along the sea, under shabby herbaceous vegetation; 972.241.
18. Amnisós, loose loam at north foot of a hedge of *Arundo donax* L. (a tall grass, 2-4 m high) along field, 972.198.
19. Agía Varvára, 21.x.1972, 700 m, pleurocarpous mosses and *Selaginella denticulata* (L.) Link, on short, almost vertical slope, northwest exposition, in phrygana; 972.199.
20. Agía Varvára, 750 m, humus-rich very stony loam with a scanty grass and *Juncus* vegetation; the spot seems to be a spring in the spring season; 972.228.
21. Agía Varvára, 750 m, opulent cushion of pleurocarpous moss on north bank of dry rivulet in degraded phrygana; 972.223.
22. Agía Varvára, 600 m, swept from low bushes (*Sarcopoterium*) in phrygana; 972.203.
23. Réthimnon, 22.x.1972, verge of a road near the city, comparatively damp, heightened rather recently with coarse (beach-?) sand, overgrown with scanty grass; 972.225.
24. Réthimnon, comparatively damp plastic yellow loam at the foot of an earthen wall about 2 m high across a field, north exposition; 972.216.
25. Drosiá, between Iráklion and Pérama, about 15 km E of the latter, 23.x.1972, crumbly loam, abundant mosses and litter under large *Quercus coccifera*, at base of north side of an east-west running ravine; 972.212.
26. Drosiá, upper 2 cm of bare compact loam, with a thin carpet of ephemeral liverworts (*Riccia*, *Fossombronina*, *Targionia*) in strongly degraded phrygana on south wall of the same ravine as 25; 972.243.
27. Drosiá, litter under large *Quercus coccifera* on south slope; 972.226.
28. Drosiá, large isotomid, walking in large numbers freely on stones, soil, etc., on south slope, collected manually; 972.214.
29. Knossós, vicinity of the excavations, 24.x.1972, crumbly yellow loam, rarely trodden, under large peach tree on north slope of brook near the "guest-house" (Xénon), undergrowth mainly *Oxalis pes-caprae* L.; 972.242.
30. Knossós, loose loam, sparsely grown with grass and *Oxalis pes-caprae* at foot of a 4 m-high cliff along road; 972.219.
31. Knossós, collected manually under stones, pieces of dead wood, etc.; 972.195.
32. Iráklion, 25.x.1972, after heavy rains, loam, litter and rotting leaf bases under vigorous ruderal vegetation (*Ecballium elaterium* (L.) Rich.); 972.233.

33. Iráklion, loam of ruderal field, overgrown mainly with grass and *Carpobothrus* along road; 972.232.
34. Iráklion, bank of loam overgrown with strongly ruderal vegetation; 972.244.
35. Máraithos, 15 km W of Iráklion, 26.x.1972, litter under *Pistacia lentiscus* in phrygana on weak north slope; 972.209.
36. Máraithos, upper 2 cm compact bare loam, with ephemorous vegetation of liverworts (*Fossombronina*) and seedlings, along roadside; 972.231.
37. Máraithos, litter under large *Ceratonía siliqua* L. in field; 972.237.
38. Máraithos, collected manually from stones and pieces of wood, and swept from *Pistacia lentiscus*; a *Seira* on an olive trunk; 972.196.
39. Máraithos, large extremely numerous isotomids, walking on stones and on bare soil; 972.204.
40. Amnisós, 27.x.1972, upper cm loam along beach, with very spare vegetation of *Salicornia fruticosa* (L.) L., some annual mosses (*Bryum* spec.), near *Tamarix* bush; 972.200.
41. Amnisós, loamy sand of fallow field with a mat of *Malva* spec.; 972.235.
42. Gázi, 7 km W of Iráklion, 28.x.1972, loamy clay under *Ecballium* in fallow field 500 m from the shore; 972.206.
43. Mália, 29.x.1972, brown, crumby, stony loam grown with a poor grass vegetation under large *Ceratonía* tree; 972.205.
44. Mália, litter of *Quercus coccifera* in well-developed phrygana; 972.211.
45. Mália, terra rossa, acrocarpous mosses and *Selaginella* deep in a rock-fissure at foot of north slope of ravine; 972.222.
46. Mália, collected manually under stones in phrygana; 972.201.
47. Agía Galíni, 14 km NW of Festós, 30.x.1972, beach sand and *Posidonia* (a kind of sea grass) debris in a layer of about 2 cm; 972.218.
48. Agía Galíni, *Tamarix* litter and fine sand, overgrown with *Malva* and *Oxalis pes-caprae* just above the beach; 972.207.
49. Agía Galíni, yellowish-brown loam of lucerne field; 972.220.
50. Agía Galíni, collected manually, under large pebbles on the beach; 972.202.

Table 1. Greek orthography and transcription of the locality names used

Κρήτη	Kríti	Ἀμνισός	Amnisós
Θέρισος	Thérisos	Ἀγία Βαρβάρα	Agía Varvára
Τσαγαράκ	Tsagarák	Ρέθυμνον	Réthimnon
Ἡράκλειον	Iráklion	Δροσιά	Drosiá
Γιόφυρος	Giófiros	Πέραμα	Pérama
Φεστός	Festós (in Times Atlas Phaistos)	Κνωσός	Knossós
Γερω-Πόταμος	Geropótamos	Μάraithος	Máraithos
Φορτέτσα	Fortétsa	Γάζιον	Gázi
Ιούχτας	Iouchtas	Μάλια	Mália
Ἀρχάνες	Archánes	Ἀγία Γαλήνη	Agía Galíni

## ACCOUNT OF THE SPECIES

## ONYCHIURIDAE

***Metaphorura affinis* (Börner, 1902) (Fig. 1)**

Material: see table 2.

Discussion. The rather extensive material of this common European species that I could study is strongly heterogenous in some characters of the apex of the abdomen. The material can be separated into two forms, A and C, connected by a few intermediate specimens I shall refer to as B. For the number and distribution of these forms, see Table 2.

The forms can be segregated as follows. Specimens of form A have the dorsal granulation on abd<sub>5</sub> so strongly developed that the secondary granulations touch each other, giving a roughly hexagonal outline (Fig. 1d). Between the macrochaetae p<sub>2</sub> on abd<sub>5</sub>, ten such coarse granules are present. The granules also have a distinctly flattened apex, as can be seen in profile. The same type of integumentary ornamentation is visible on the dorsal surface of head, thorax, and abd<sub>1-4</sub>. On abd<sub>6</sub> the granules are not flattened or hexagonal, but more or less globular. Laterodorsally, abd<sub>6</sub> shows an area where these granules are grossly enlarged (Fig. 1c). Furthermore, specimens of this type invariably have the sensilla s on abd<sub>5</sub> very short — in fact, reaching only to about the middle of the pseudocellus of abd<sub>5</sub> (Fig. 1b, c). Finally, the anal spines are slightly heavier and more strongly yellow-tinted than those in the types B and C.

Specimens of type C have the integumentary granulation rather fine and regular, the granulations not touching each other and having a globular profile. Only the granulation of abd<sub>6</sub> is much coarser, but the two areas with strongly swollen granula are absent. Moreover, seta s on abd<sub>5</sub> is distinctly longer, reaching well beyond the posterior margin of the corresponding pseudocellus (Fig. 1a). As mentioned above, the anal spines seem to be more slender and paler. About 17-18 granulations are present between the p<sub>2</sub> on abd<sub>5</sub>.

The intermediate type B has the granulations enlarged, though not so strongly

Table 2. Distribution of types A, B, and C within the samples of *Metaphorura affinis*

A	B	C	sample nr.	locality
2 ♀, 1 ♂, 1 juv.			5	Festós
1 ♀, 2 ♂, 1 juv.			6	Festós
1 ♀, 1 juv.		1 juv.	24	Réthimnon
1 ♀, 1 juv.			48	Agía Galíni
5 ♀, 1 ♂			49	Agía Galíni
1 ♀, 2 juv.			30	Knossós
	3 ♀		29	Knossós
	1 ♀		16	Amnisós
		1 juv.	9	Fortétsa
		1 ♀	14	Iouúctas
		2 ♀, 2 juv.	20	Agía Varvára
		3 ♀, 1 ♂, 1 juv.	45	Mália

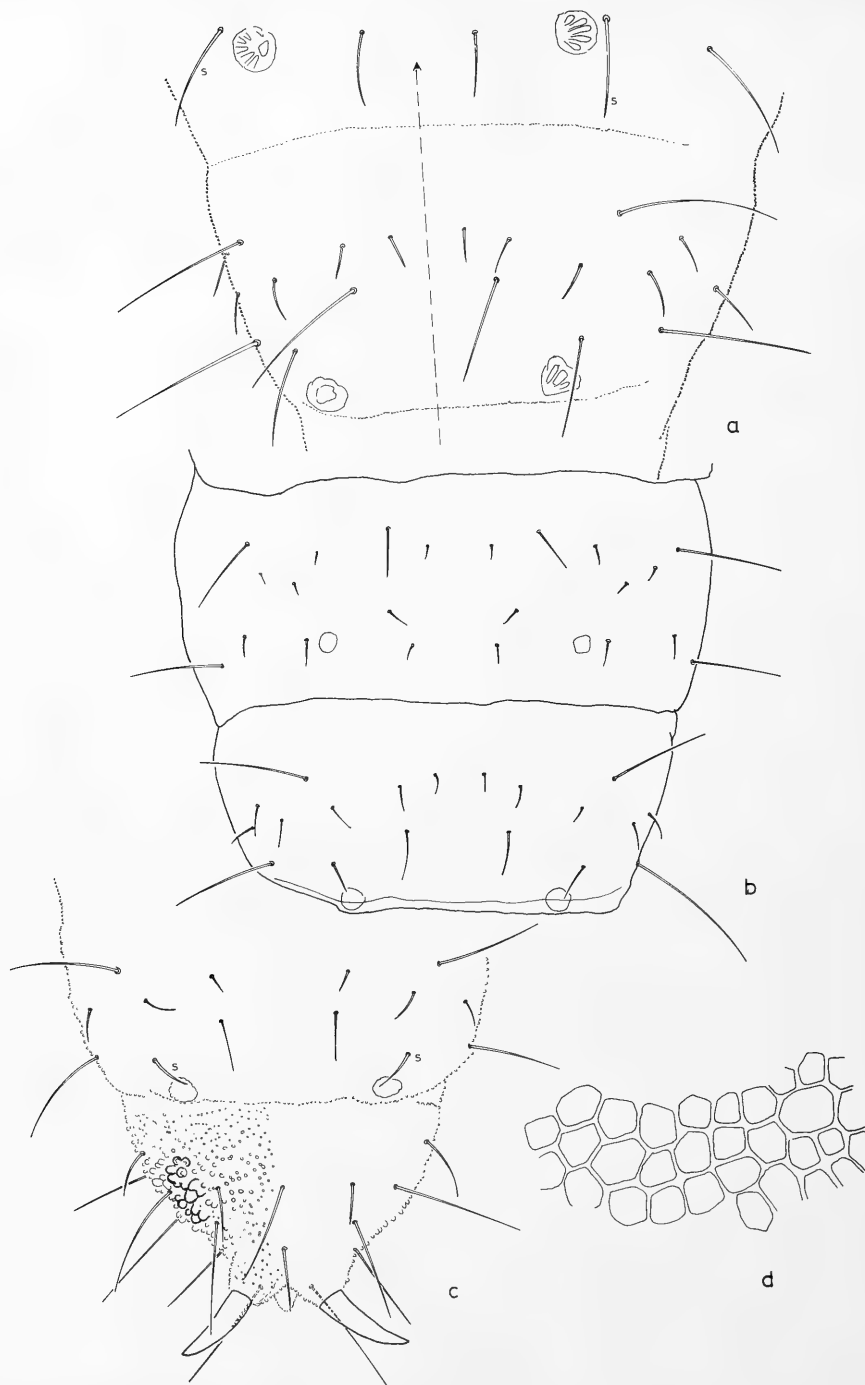


Fig. 1. *Metaphorura affinis* (Börner). a, abd<sub>5</sub> of type C ♀; b, abd<sub>4-5</sub> of type A ♀; c, abd<sub>5-6</sub> of type A ♀ (on abd<sub>5</sub> setae a<sub>1</sub> omitted); d, hexagonal arrangement of secondary granulations between p<sub>2</sub>-p<sub>2</sub> on abd<sub>5</sub> of type A ♀ (very strong magnification)

as in type A (between the  $p_2$  on  $abd_5$  there are about 12 granulations), and they are only slightly hexagonal in outline and flattened at the top. On  $abd_6$  the strongly enlarged lateral granulations are completely or almost absent. Seta  $s$  on  $abd_5$  is just as short as in type A. Evidently, type B is much closer to type A than to type C, and it could be argued that A and B should be united.

Börner (1902) described his *Tullbergia affinis* from many specimens from Sicily and Calabria, and called the integumentary reticulation „fein und gleichmässig, nur auf dem Kopfe ein klein wenig kräftiger“. His material thus seems to agree with my form C.

I have checked the other material of this species in our collection. Material from Iceland, Sweden, Austria, and the ČSSR proved to be referable to form B; material from Yugoslavia, as well as the specimens recorded by me from Rhodes, are identifiable as belonging to C.

As far as I know, form A, which seems to deviate the most from typical *affinis*, cannot be correlated with any species description. The drawing made by Handschin (1929) of  $abd_6$  of his *Tullbergia bipartita* shows a perfectly simple granulation, only compatible with type C.

Cassagnau (1963) described a comparable diversity in granulation in material of *M. bipartita* (Handschin, 1920) from North Africa: some specimens, considered to be aberrants, showed a remarkably coarse granulation (consisting of rounded papillae) all over the body (also the ventral face?), whereas  $abd_6$  bore the two types of enlarged granulations described above. Moreover, the unpaired, conical organ on  $abd_6$  was reduced to at most a vague boss. The last observation differs widely from what I found in Cretan material, where the unpaired cone is well-developed in all forms.

I admit that the complex situation described above could be explained by assuming the presence of two species, *affinis* and *bipartita*, in the present material. But I did not succeed in discerning the particular bilobation in the elements of the postantennal organ said to be characteristic for *bipartita*; I even wonder whether these structures are visible at all with light microscopy, and I am inclined to share Gisin's (1944) opinion that the two taxa are synonymous.

As is evident from Table 2, the three types cannot be simply related to sex or maturity. However, since some very young specimens have seta  $s$  strongly developed on  $abd_5$  and a reticulation of type C, it is possible that type A concerns specimens that are not only sexually mature but also completely full-grown.

Cassagnau (l.c.) brought the described phenomena into tentative correspondence with ecomorphosis. This possibility merits closer consideration, although the seemingly normal fat body, the full intestine, and the apparent sexual maturity of many specimens of form A all argue the contrary. However, this suspicion and the fact that intermediate forms between the extremes occur in Crete and elsewhere, make it impossible, at present, to attribute specific status to types A and C. Their virtually sympatric occurrence within Crete is sufficient reason not to create subspecies.

One female from sample 29 is aberrant in that it completely lacks the anal spines. The median process is present however.

**Metaphorura spec. (Fig. 2)**

Material: one immature specimen from sample 30.

Discussion. The single specimen, measuring 0.6 mm, is so immature that no trace of a genital orifice is visible. It is very unfortunate that more and better material is not at hand, since the specimen shows some interesting features.

The 6th abdominal segment has 2+2 spines, and therefore identification as a *Stenaphorura* seems appropriate (Fig. 2a). The relatively small postantennal organ, with a small number of elements (Fig. 2b), the structure of ant<sub>4</sub>, and the pseudocellar formula 11/122/22221 point toward identity with *Tullbergia* (*Stenaphorura*) *gisini* Selga, 1963, described from the Sierra de Guadarrama. Seemingly, the chaetotaxy of the Greek specimen is in good agreement with the Spanish material. However, there are the following important differences:

- (i) the Greek specimen has an unguiculus (of about 1/3 unguis);
- (ii) the accessory sensilla in antennal organ III is lacking;
- (iii) the ant. org. III is covered by three high, thin skin flaps (Fig. 2 c);
- (iv) the postantennal organ is simple in outline;
- (v) the apex of abd<sub>6</sub> bears a tubercle which is completely comparable to that of *Metaphorura* (though slightly lower than is usual in *M. affinis* which in this respect is notoriously variable).

A median tubercle as in *Metaphorura* is described by Gisin (1963a) in his *Tullbergia novemspina* from Yugoslavia; judging from the figures given by Gisin, however, this species differs not only by having 4+4 lateral spines on abd<sub>6</sub>, but also by a very different chaetotaxy of abd<sub>6</sub>.

**Neotullbergia tricuspis (Börner, 1902)**

*Tullbergia ramicuspis* Gisin, 1953, 1960, Dallai, 1973 (nec *T. tricuspis*: Gisin, 1944, 1960).

Material: 1 ♀ from sample 24.

Discussion. The species has been recorded from central and southern Europe (Spain, Italy, France, Yugoslavia). The single specimen from Crete agrees well with the description of *ramicuspis* by Gisin (1953), but the anal spines may be a bit more slender.

The complicated synonymy of this species has been clarified by Hüther (1961). However, another problem of synonymy still has to be settled. Bonet (1944) recognized in *Lipura pusilla* Giard, 1895 (description corrected in Giard, 1896; note also that Bonet mentions wrong publication dates) a *Neotullbergia*. He was not able to locate this species, but among material from Chili Rapoport & Rubio (1963) found a species that fitted Giard's description. These authors overlooked Giard's remark that he knew *L. pusilla* not only from material from Chili but also from Cape Gris Nez in NW France. This fact, the scanty description, and the small size (0.6 mm) of *pusilla*, all favour the supposition that *pusilla* might be, at least partially, immature *tricuspis*. To preclude the annoying complications that would result, I herewith restrict the type locality of Giard's species to Santa Rita, Chili.

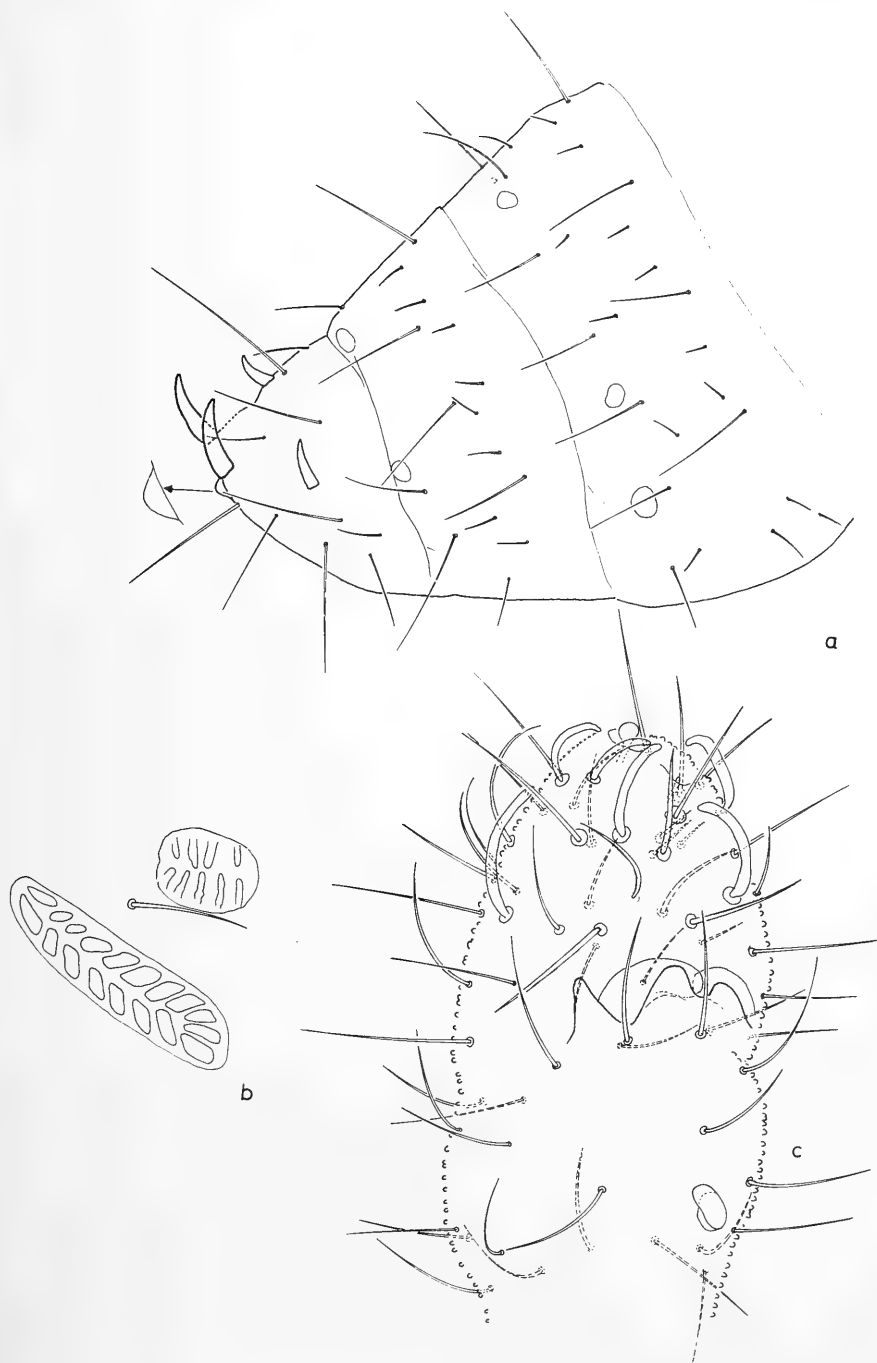


Fig. 2. *Metaphorura* spec. a, abd<sub>4-6</sub>; b, postantennal organ and neighbouring pseudocellus; c, antenna<sub>3-4</sub>

**Mesaphorura critica n. sp. (Fig. 3)**

Material: sample 6: 1 ♀; 20: 6 ♀; 23: 1 ♀; 24: 5 ♀ and 2 juv.; 25: 3 ♀ and 2 juv.; 27: 1 ♀; 33: 1 ♀; 49: 2 ♀. The ♀ from sample 23 is selected as holotype.

Description. Habitus as usual in the genus; total length about 0.4 mm. Granulation fine and regular, a bit coarser on abd<sub>6</sub>.

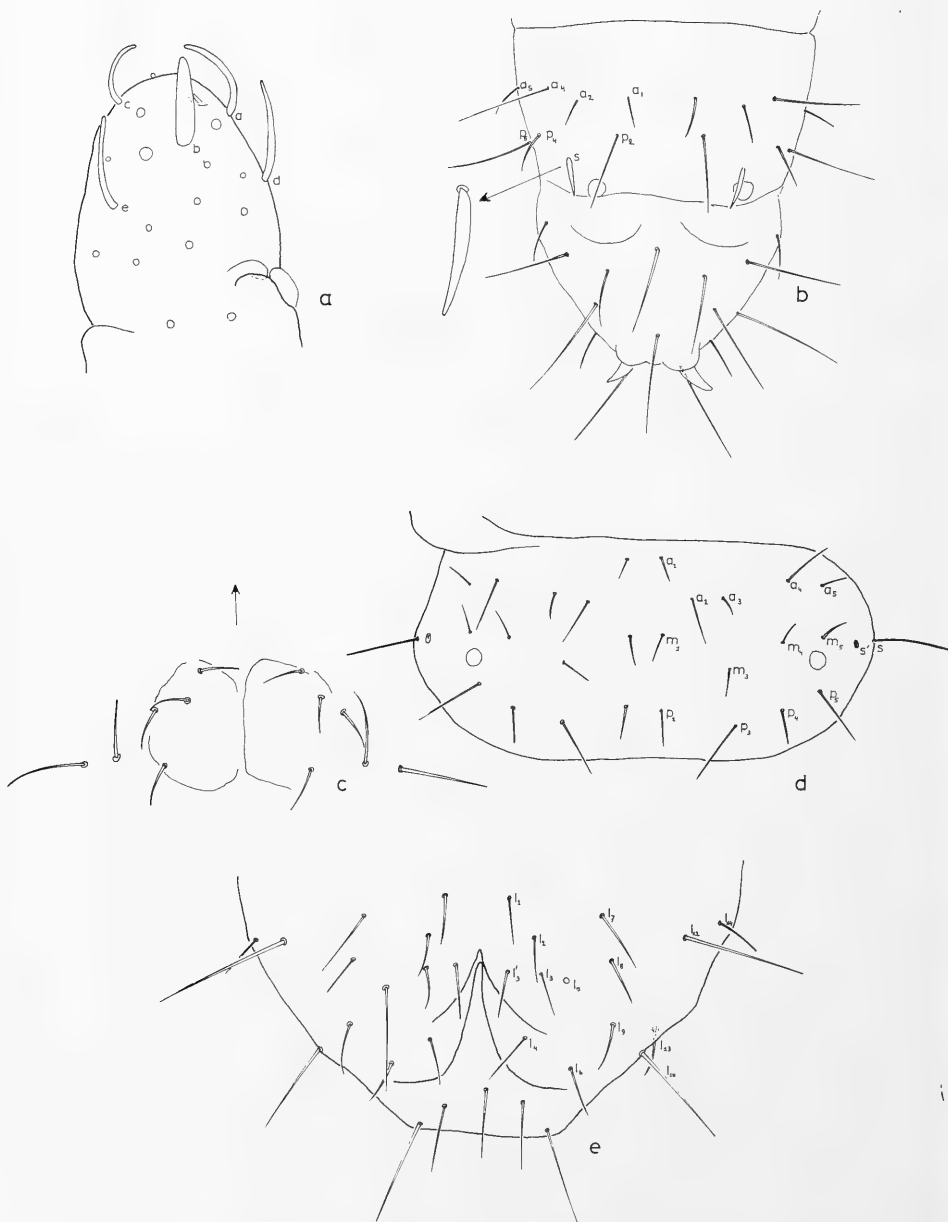


Fig. 3. *Mesaphorura critica* n. sp. a, ant<sub>4</sub>; b, abd<sub>5-6</sub>; c, ventral tube; d, th<sub>3</sub>; e, chaetotaxy of anal region



Chaetotaxy:  $th_1$ ;  $m_{1-4}$ ;  $th_2$ ;  $a_{1-5}$ ,  $m_1$ ,  $m_{3-5}$ ,  $s'$ ,  $s$ ,  $p_1$ ,  $p_{3-5}$ ;  $th_3$ ; as  $th_2$  (Fig. 3d);  $abd_1$ ;  $a_{1-5}$ ,  $m_4$ ,  $p_{1-5}$ ;  $abd_2$  idem;  $abd_3$  idem;  $abd_4$ ;  $a_{1-4}$ ,  $m_4$ ,  $p_{1-5}$ ;  $abd_5$ ;  $a_1$ ,  $a_{3-5}$ ,  $p_2$ ,  $s$ ,  $p_{4-5}$ . Distinct macrochaetae on  $abd_4$  are  $a_2$  and  $p_2$ , on  $abd_5$   $a_4$  and  $p_2$ . Anal flaps without setae  $l'_2$  (Fig. 3 e).

Rosette-shaped pseudocelli distributed as 11/011/10011; those on  $th_2$  and  $th_3$  are situated between setae  $m_3$  and  $p_3$ .

Antennae with the normal sensory complement. Sensilla b thick (Fig. 3a). Ant: head  $\varnothing$  = ca. 0.65. Postantennal organ about 1.5-2 times pseudocellus. Labium with 4+4 setae. On  $th_{2-3}$  the "Lateralsensille"  $s$ , distinguished by Rusek (1971b) not differentiated from a normal hair; sensillae  $s'$  present on these segments. Sensilla  $s$  on  $abd_5$  swollen, 9.8  $\mu$  (for comparison: the length of seta  $p_2$  on this segment is 16  $\mu$ ).

Claw toothless, 8.5  $\mu$ , unguiculus needle-like, 3  $\mu$ .

Semicircular ridges on  $abd_6$  evident, anal spines 6  $\mu$ , curved (Fig. 3b).

Ventral tube with 4+4 apical setae, 1 laterobasal, and 1 lateral seta (Fig. 3c).

Discussion. The material under consideration is exactly intermediate between *M. italica* and *M. sylvatica*, both described by Rusek (1971) from Italy, the ČSSR, and Bulgaria. The material is identical to *M. italica*, except for the lack of seta  $a_2$  on  $abd_5$ ; otherwise it is identical to *M. sylvatica*, but the pseudocellus on  $th_3$  is situated between setae  $m_3$  and  $p_3$ .

The above situation might either be interpreted as an indication of synonymy of *italica* and *sylvatica* or necessitate the description of a new species. The perfect uniformity of all specimens studied from Crete finally persuaded me to choose the second alternative.

The specific name refers to the ambiguous state of the new species, alluding at the same time to the Greek name Kriti.

### **Mesaphorura italica** (Rusek, 1971)

Material: sample 11: 1 juv.; 17: 4 ♀; 23: 1 ♀; 24: 1 ♀; 25: 3 ♀; 30: 1 ♀; 35: 1 ♀.

The material is in full agreement with Rusek's detailed description. The species was subsequently recorded by Rusek (1973b: Italy) and by Ellis (1974: Rhodes).

### **Mesaphorura krausbaueri** Börner, 1901

Material: sample 40: 11 ♀ and 2 ♂; 43: 1 ♀.

Description. The material differs consistently from the description given by Rusek (1971) in one respect: in all specimens studied seta  $l'_2$  is present on the anal flaps. However, this is not only the case in Greek material: a casual study of some Dutch specimens showed that this seta is also present there.

Since the delimitation of this species has been drastically narrowed by Rusek's work, it is impossible to say much about its geographical distribution. As conceived of at present, it is known from the ČSSR, Italy, the Netherlands, and Crete. The occurrence of males in the Cretan material is noteworthy.

To synthesize the knowledge of the *krausbaueri* group, I constructed the following, simple key to the species.

Key to the species of the *Mesaphorura krausbaueri* group

1. abd<sub>5</sub> in frontal row with 1 + 1 microchaetae between bordering macrochaeta (a<sub>2</sub> in this case) . . . . . *hygrophila* (Rusek, 1971)
  - 2 + 2 microchaetae between bordering macrochaeta a<sub>4</sub> . . . . . 2
  - 3 + 3 microchaetae between bordering macrochaeta a<sub>4</sub> . . . . . 3
2. pseudocellus on th<sub>3</sub> behind or between p<sub>3</sub> and p<sub>4</sub> . . . . . *sylvatica* (Rusek, 1971)
  - this pseudocellus between m<sub>3</sub> and p<sub>3</sub> . . . . . *critica* n. sp.
3. th<sub>3</sub> with 2 + 2 pseudocelli . . . . . 4
  - th<sub>3</sub> with 1 + 1 pseudocelli . . . . . 5
4. all sensillae strongly developed; in particular sensilla b on ant<sub>4</sub> inflated . . . . . *sensibilis* Rusek, 1973
  - most sensillae slender; sensilla b on ant<sub>4</sub> thin . . . . . *tenuisensillata* Rusek, 1974
5. pseudocelli on th<sub>2-3</sub> situated between m<sub>3</sub> and p<sub>3</sub> . . . . . *italica* (Rusek, 1971)
  - these pseudocelli between or behind p<sub>3</sub> and p<sub>4</sub> . . . . . 6
6. on abd<sub>4</sub> p<sub>1</sub> is a macro-, p<sub>2</sub> a microchaeta . . . . . *krausbaueri* Börner, 1901
  - on this segment p<sub>1</sub> is a micro-, p<sub>2</sub> a macrochaeta . . . . . *yosiii* (Rusek, 1967)

**Protaphorura prolata** (Gisin, 1956)

*Onychiurus prolatus* Gisin, 1956.

*O. sublatus* Gisin, 1957. — **nov. syn.**

*O. gisini* Haybach, 1960. — **nov. syn.**

*O. prolatus conlatus* Gisin, 1962. — **nov. syn.**

*O. prolatus trilatus* Gisin, 1963b. — **nov. syn.**

Material: sample 9: 4 ♀ and 1 ♂; 18: 8 ♀ and 10 ♂; 20: 1 juv.; 21: 1 ♂ and 1 juv.; 24: 9 ♀, 11 ♂ and 12 juv.; 30: 8 juv.; 31: 1 ♀; 32: 6 ♀ + 36 ex. in alcohol; 34: 5 ♀, 3 ♂ and 1 juv.; 36: 1 ♂ and 1 juv.; 37: 12 ♀ and 3 ♂; 38: 6 ♀, 7 ♂ and 12 juv.; 44: 1 juv.

Discussion. The extensive material (in all 125 specimens) is very homogenous, and variation is not much greater between samples than within samples. The largest specimens measure 1.8 mm, but adult specimens are normally 1.3 mm long.

The dorsal pseudocellar arrangement was found to be very constant, viz., 33/022/33343. In fact, not a single deviation from this formula was noted. The lack of a tooth on the unguis is also constant. Absence of seta m on th<sub>1</sub> was doubtful only once (it did occur in one adult specimen, and only asymmetrically). Seta i is sometimes missing, especially in immature material. Much more variable is the number of microchaetae in hind row of th<sub>1</sub>. Rather often, only two were found (although almost always asymmetrically, the higher number being present on the other half of the segment). At the base of the ventral tube, 2 + 2 setae are usually present, but an arrangement 1 + 1 occurs relatively frequently. Abd<sub>3</sub> invariably lacks seta s'.

The shape of the anal spines, in itself difficult to assess exactly, is rather variable, ranging from rather stout to rather slender. The arrangement of the

four prespinal setae on  $\text{abd}_6$  cannot be regarded as a useful character, gradual transitions being demonstrable between almost parallel and forming a blunt angle.

The M/s ratio on  $\text{abd}_6$  (following Gisin's convention, in which the length of the anal spines is set at 10) is variable. Some random measurements, all made in adult specimens, are: sample 9: 12/7; sample 18: 11/6, 11/6, 12/6, 12/6, 13/6; sample 32: 24/11; sample 34: 18/10; sample 37: 18/11; sample 44: 18/12, 20/12, 20/10. Formidable as this may seem, it only means a shift in the length ratio of M and s from 1.5 to 2.2; often it is also difficult to measure the exact length of hairs very accurately, because they do not lie parallel to the optical plane. The same holds even more strongly for the measurement of the anal spines.

The circumstances compelled me to recognize a rather iconoclastic set of new synonymies.

*Onychiurus sublatius* Gisin, 1957, was described after an unstated number of specimens from Austria and England. The species was considered to differ from *Onychiurus prolatus* (1) because of its smaller size, viz., 1.4-1.85 mm as against 2.3-2.6 mm in *prolatus*, (2) because the anal spines and claw are plumper in *sublatius*, and (3) because  $M/s = 24/7-8$  (in *prolatus* originally given as 21/9, but in Gisin (1960) "as in *latus*", which would mean 29/10).

*Onychiurus gisini* Haybach, 1960, described from Austria, was contrasted with *O. cancellatus* Gisin, 1956, because the prespinal setae of  $\text{abd}_6$  were said to delineate two strongly convergent lines. Apart from this character, the doubtful value of which is discussed above, there is no essential difference from *O. prolatus*.

*Onychiurus prolatus conlatus* was described by Gisin (1962) after material from caves in eastern Switzerland (*prolatus prolatus* was described originally from caves in the Savoy Alps and the Swiss Jura). Differentiating characters are (1) M/s ratio 19/14 (instead of 21/9), (2) a difference in shape of  $\text{abd}_6$  (as seen in profile) and (3) the four prespinal microchaetae of  $\text{abd}_6$  forming two slightly converging lines. (Gisin adds here that he had also observed this in a typical population of *prolatus*!)

*Onychiurus prolatus trilatus* was described by Gisin (1963b) from caves in France (Drôme). The subspecies was characterized by having two instead of one median hair on the tergum of  $\text{abd}_6$ ; however, at least three adult specimens from Crete show this same character.

### ***Onychiurus pseudoghidinii* Dallai, 1969 (Fig. 5a)**

Material: sample 4: 1 adult and 2 subadult ♂.

Discussion. The adult specimen clearly demonstrates the (only) character that distinguishes *pseudoghidinii* from *ghidinii* Denis, 1938, viz., the third pair of pseudocelli at the ventral face of the head (Fig. 5a). However, in one of the subadult specimens these pseudocelli are greatly reduced, and in the other they are absent. In my opinion, this casts some doubt on the validity of Dallai's species, but in view of the paucity of my material I must limit myself to drawing attention to the imminent synonymy.

*O. pseudoghidinii* is described from the Isle of Montecristo (about 50 km S of Elba); *ghidinii*, described from the north of Italy, is also known from France,

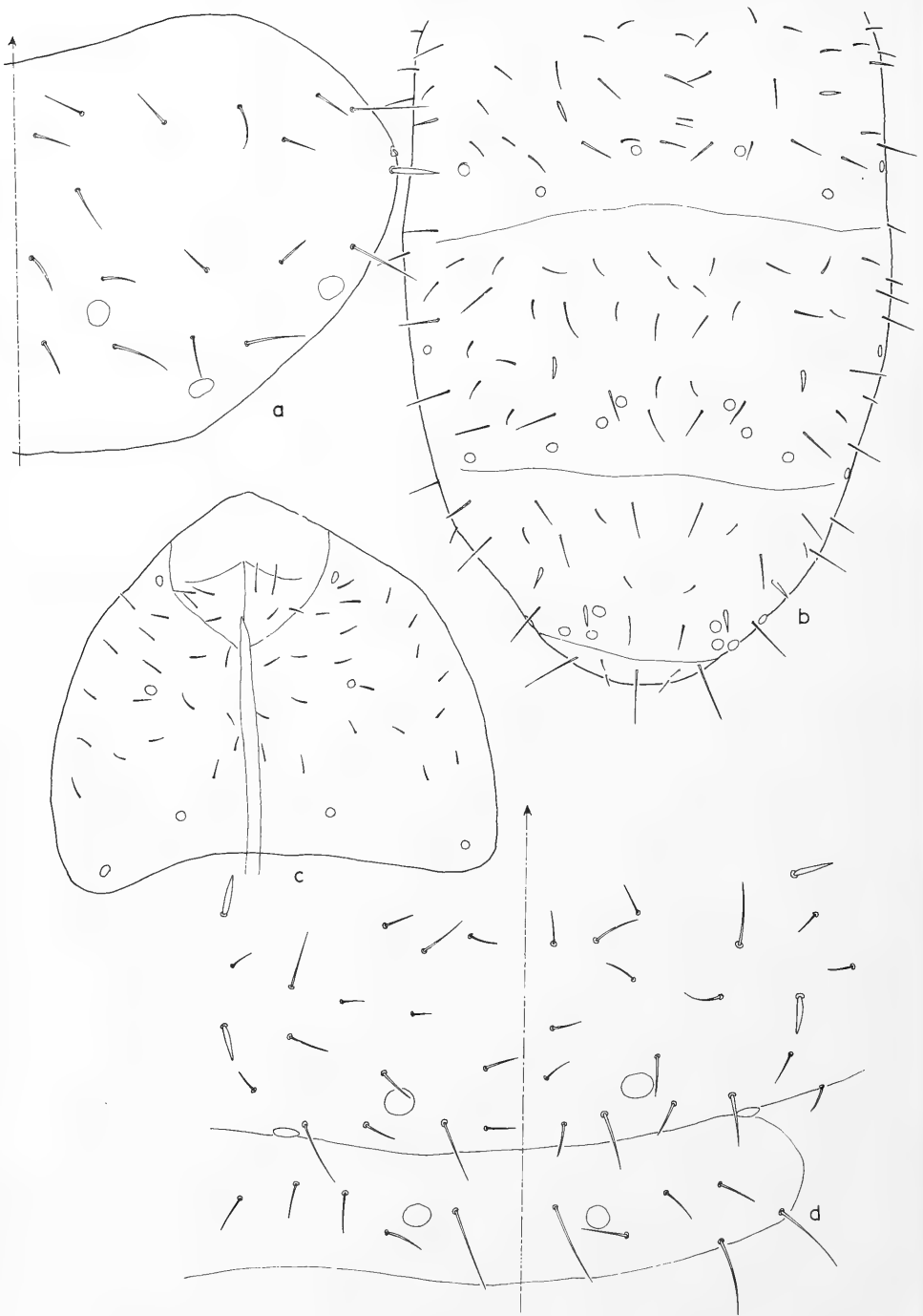


Fig. 4. *Onychiurus xenonis* n. sp. a,  $th_2$ ; b,  $abd_{3-6}$ ; c, ventral aspect of head; d, posterior margin of head and  $th_1$ .

Switzerland, Bulgaria, Morocco, Madeira, and the Azores. Material from the last locality has been described in detail by Hüther (1970). The material now under consideration coincides completely with Hüther's description, except that the granulation of the Greek material seems to be somewhat less developed.

In one specimen antennal organ III was guarded in both antennae by only four papillae. The other two specimens had the normal number (five).

***Onychiurus* cf. *stachianus* Bagnall, 1939**

Material: sample 6: 1 ♀; 24: 1 juv.

Description. The single adult specimen measures 1.2 mm. It agrees with the description of *stachi* Denis, 1938 (nec Bagnall, 1935, rebaptized *stachianus* by Bagnall (1939)), except that the unguis has no lateral teeth. In the absence of adult males the identification can, of course, only be tentative.

The species was described from the Postumia cave in Yugoslavia; it has been recorded from the ČSSR by Rusek (1959), from England by Goto (1953), and from Spain by Selga (1962a). Confusion with *O. pseudostachianus* Gisin, 1956 (= *stachianus* sensu Gisin, 1952) in these records cannot be ruled out, however.

***Onychiurus xenonis* n. sp. (Fig. 4)**

Material: sample 29: holotype ♀ and 6 ♀, 3 ♂, paratypes.

Description. Length only 0.6 mm. White, integument finely and regularly granulated. Antennal bases not differentiated. Differentiation into micro- and macrochaetae weakly developed; some setae swollen to the shape of sensillae. No anal spines.

Antenna<sub>4</sub> with small retractile papilla and sensilla in a groove above ant. org. III. The latter consists of 5 setae, 5 slender papillae, 2 straight rods, and 2 curved smooth sense clubs. Postantennal organ compound, with about 12 primary tubercles. Claw without inner or lateral teeth, unguiculus gradually tapering to a slender apex, reaching tip of unguis. No trace of furca.

On head and on all body segments except th<sub>1</sub> and abd<sub>6</sub>, one or two pairs of hairs are swollen and have acquired the shape of sensillae or small spinules. On the head two such pairs are present, not far from the hind margin (Fig. 4d). Also th<sub>2-3</sub> each have a pair of such setae, which are situated laterally, just dorso-caudad to the lateral sensilla, which is apparently characteristic for all Onychiuridae and Hypogastruridae (Fig. 4a). Abd<sub>1-4</sub> each have two pairs, one of which is situated in about the middle of the width of the segment anterior to the second pseudocellus from the median, whereas the second pair of sensillae lies antero-laterally from the third pseudocellus (Fig. 4b). Abd<sub>4</sub> has only one pair, situated in front of the third pair of pseudocelli, and abd<sub>5</sub> again has two pairs, one near the anteromedian (first) pair of pseudocelli, the second anterior to the fourth pair of pseudocelli. On the sternite of abd<sub>4</sub>, two indistinct pairs of these sensillae are present in front of the pseudocelli. Ventral tube with 6 + 6 setae.

Pseudocelli: Dorsal arrangement of pseudocelli 32/133/33354, ventral arrangement 4/000/2222. The 4th pseudocellus under the head is situated near the lateral

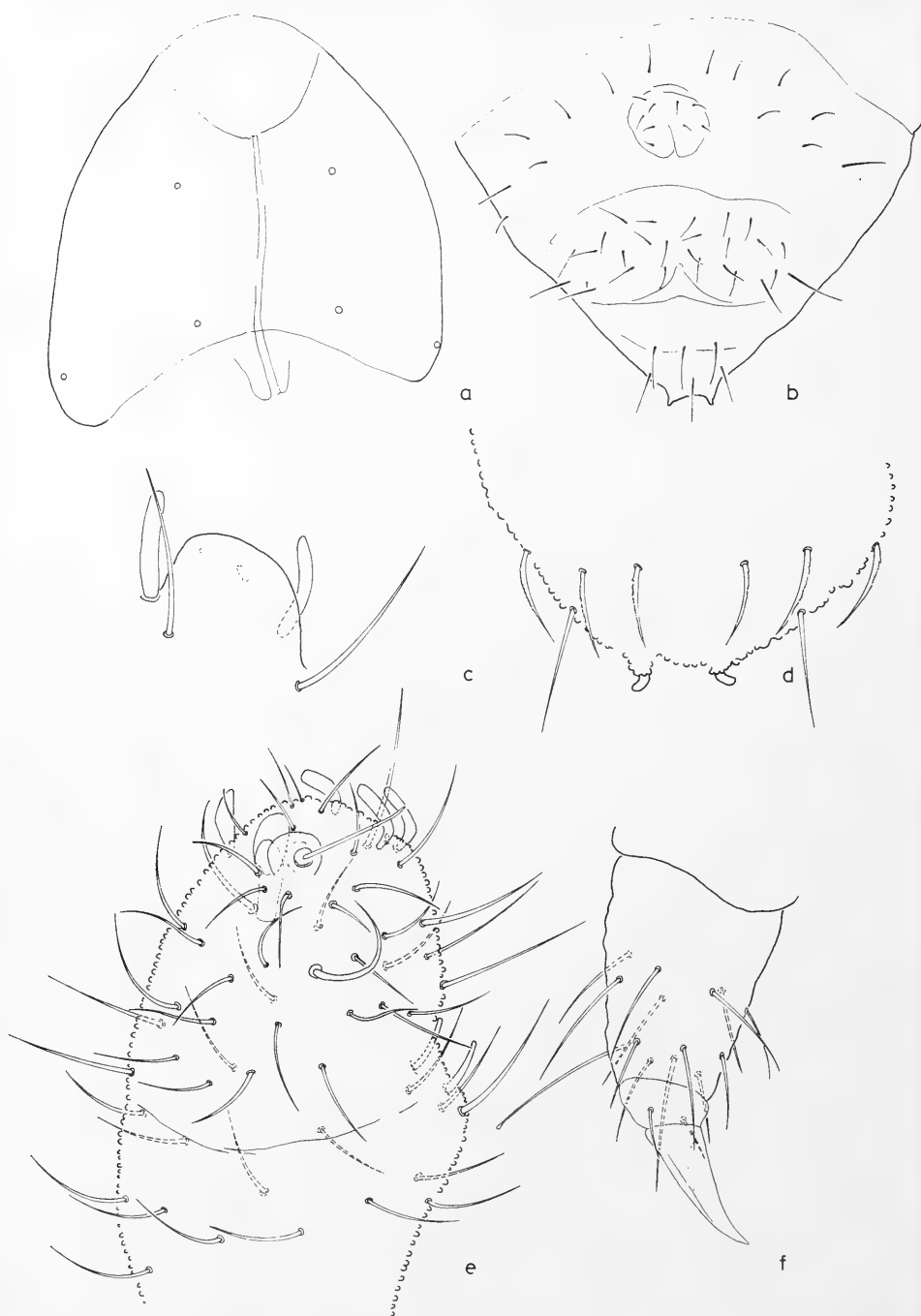


Fig. 5. *Onychiurus pseudoghidinii* Dallai, a, pseudocelli on ventral face of head. *Acheroxenylla cretensis* n. sp. b, ventral chaetotaxy of abd<sub>3-6</sub>; c, antennal organ III; d, abd<sub>6</sub> dorsally; e, ant<sub>3-4</sub>; f, claw of P<sub>3</sub>

border of the labium. The pseudocellus is slightly oval and easily overlooked (Fig. 4c).

In the male specimens no male organ is discernible.

**Discussion.** The new species belongs to the *Onychiurus* (s. str.) complex of species, having normal unguiculi, smooth sense clubs in the antennal organ, and at the same time lacking anal spines. The species is conspicuous in having no less than 4 pseudocelli on the ventral face of the head, and also in possessing a number of spine-like "sensillae". This last character suggests a relationship to *O. edinensis* Bagnall, 1935, according to Murphy (1960) the valid name for *O. spinularius* Gisin, 1952. This species, however, possesses strong anal spines.

The fourth ocellus at the ventral face of the head is situated close to the lateral edge of the labium, and is easily overlooked. Nevertheless, *xenonis* is not easily confused with the species with which it seems otherwise to be most related with respect to the arrangement of the pseudocelli, e.g. *O. dunarius* Gisin, 1956.

## HYPOGASTRURIDAE

### *Acheroxenylla* n. gen.

**Diagnosis.** Homochaetotic Hypogastruridae. Antennae with retractile papilla, 3 outer and 1 inner cylindrical sense hairs. Postantennal organ, unguiculus, furca, and retinaculum absent. Ocelli 2+2. Tibiotarsi with 2 tenent hairs. Anal spines present.

**Type species:** *Acheroxenylla cretensis* n. sp.

This is another small genus of xenylline stock. Clearly, it is a close relative of *Xenylla*, as is evident from the absence of a postantennal organ, number and location of sense hairs on ant<sub>4</sub> and of tenent hairs on tibiotarsus, absence of the unguiculus, and the general appearance of the chaetotaxy.

However, in *Xenylla* total absence of a furca is rare; Salmon (1944) created the genus *Propexenylla* for one species having this character. But there is a complete gradation between fully developed furca (for *Xenylla*, anyway), through *X. boernerii* Axelson, to *X. acauda* Gisin and *Propexenylla atrata* Salmon. Consequently, I agree with Da Gama (1969) and place *atrata* in *Xenylla*.

The reason why I nevertheless separate *A. cretensis* from *Xenylla* lies in the number of ocelli. In almost all species of *Xenylla* (roughly 60) the number of ocelli is 5+5; in a few instances it is 4+4. I feel that inclusion of *cretensis* would unduly enlarge the scope of *Xenylla* in this respect.

Within the genera derived from *Xenylla* having fewer than 5+5 eyes, *Acheroxenylla* comes closest to *Acherontiellina* Salmon, 1964. This genus was recently redefined by Djanaschvili (1971a, b) as having cylindrical sensillae on ant<sub>4</sub>, possessing anal spines, and completely lacking the furca. Yet *cretensis* is placed in a genus of its own, to avoid disturbing the homogeneity of *Acherontiellina* and its near relative *Acherontiella* Absolon, 1913, both of which comprise only eyeless forms.

Key to the genera of the *Xenylla* group:

1. ocelli 8+8 . . . . . *Biscoia* Salmon, 1962
- ocelli 5+5 . . . . . *Xenylla* Tullberg, 1869
- ocelli 2+2 . . . . . *Acheroxenylla* n. gen.
- ocelli 0+0 . . . . . 2
2. furca completely absent . . . . . 3
- furca more or less reduced, but present . . . . . 5
3. anus nearly ventral . . . . . *Xenyllina* Delamare Deboutteville, 1948
- anus terminal . . . . . 4
4. sensillae on ant<sub>4</sub> about spherical, anal spines absent . . . . .
- sensillae on ant<sub>4</sub> about cylindrical, anal spines present . . . . .
- . . . . . *Acherontiella* Absolon, 1913
- . . . . . *Acherontiellina* Salmon, 1964
5. mucro not separated from dens, or absent; sensillae on ant<sub>4</sub> cylindrical . . . . .
- . . . . . *Acherontides* Bonet, 1945
- mucro separated from dens; sensillae on ant<sub>4</sub> conical, sometimes oval . . . . .
- . . . . . *Pseudacherontides* Djanaschvili, 1971

This key is essentially based on the work of Djanaschvili (1971a, b). I must add that I am not certain as to the inclusion of *Biscoia* in this group. The high eye-number, the presence of an unguiculus, the well-developed dens, and the peculiar antennal organ III, argue against its inclusion. I have nevertheless included the genus in this key, because it is reported to lack the postantennal organ.

***Acheroxenylla cretensis* n. sp. (Fig. 5 b-f, 6-8)**

Material: sample 1: 21 ♀, 32 ♂ and 2 juv.; 11: 18 ♀, 13 ♂ and 5 juv.; 17: 7 ♀; 26: 6 ♀, 1 ♂ and 1 juv.; 27: 1 ♂ and 3 juv. Moreover preserved in alcohol, not studied in closer detail, from sample 1: 196 specimens, 11: 210 specimens (mixed with some *Acherontiellina* that cannot be distinguished habitually), and from sample 17: 27 specimens. The holotype is a ♂ from sample 1.

Description. Length 0.7 mm. White; pigment absent, except for a few pigment granules clustered around the separate ocelli and occurring only in a few specimens. Integument coarsely granulate, especially on dorsal parts of thorax and abdomen. Hair cover not differentiated in micro- and macrochaetae, only setae distinctly longer than the others. Anal spines short and curved, on hardly differentiated papillae. Hairs smooth and simple, except the row of 3+3 setae on abd<sub>6</sub>, which are conspicuously serrate on their anterior surface (Fig. 5d).

Antennae about 5/6 times head diagonal. Ant<sub>4</sub> with large retractile papilla, and 3 outer as well as 1 inner nearly cylindrical, swollen sensory hairs. Between the group of 3 there is at least one other, very small, sensilla, difficult to observe. Of the cover of apparently normal setae on ant<sub>4</sub>, one subapical seta is inserted on some sort of wart flanking the pit of the retractile papilla (Fig. 5e). Antennal organ III consists of two long and slender sensillae, each guarded by a seta. Between the



long sensillae there is an integumentary flap that protects two small sensillae (Fig. 5c).

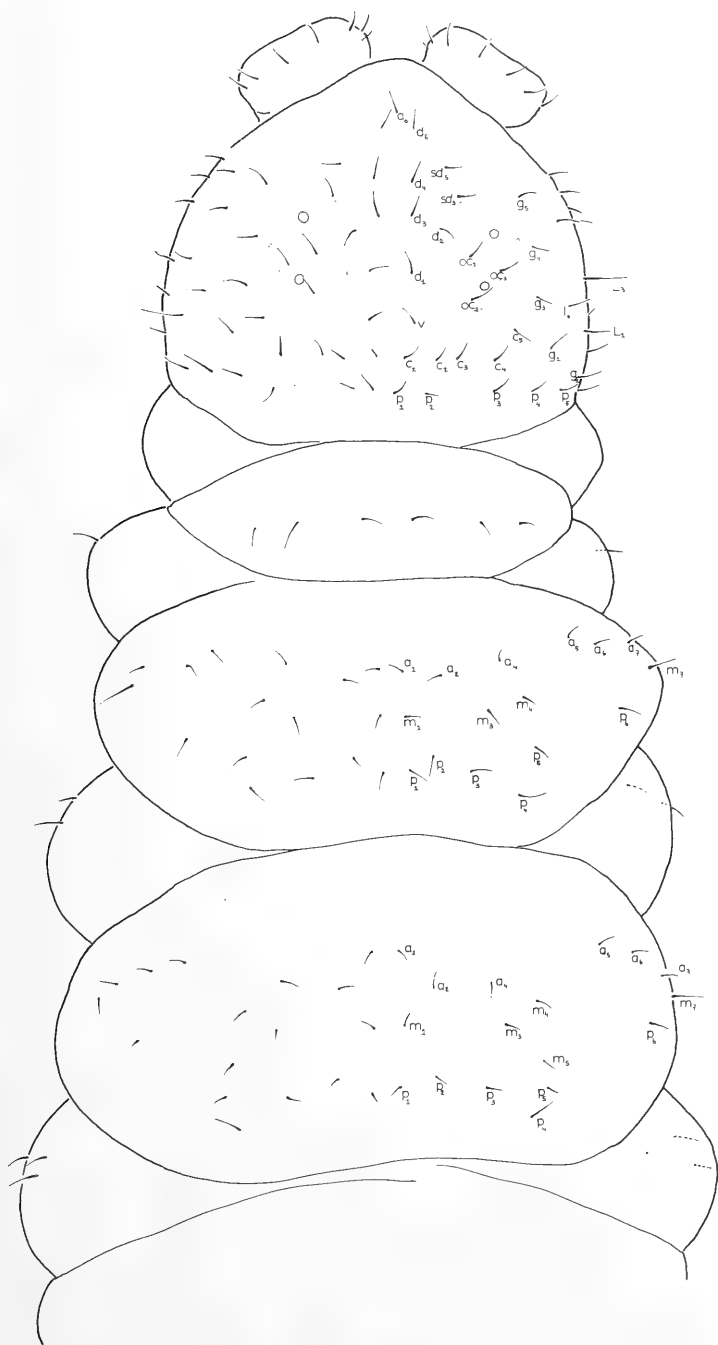


Fig. 6. *Acheroxenylla cretensis* n. sp. dorsal chaetotaxy of head and thorax

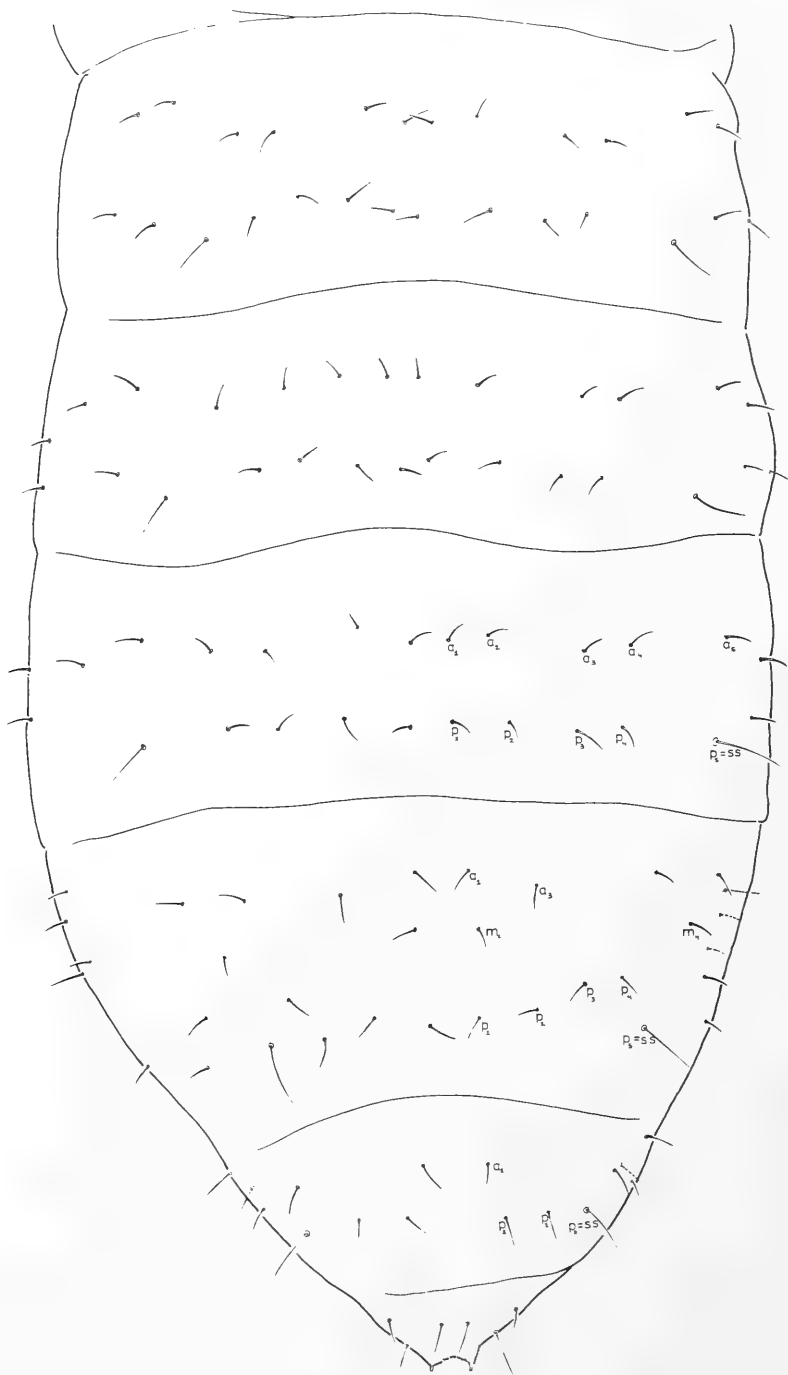


Fig. 7. *Acheroxenylla cretensis* n. sp. dorsal chaetotaxy of abdomen

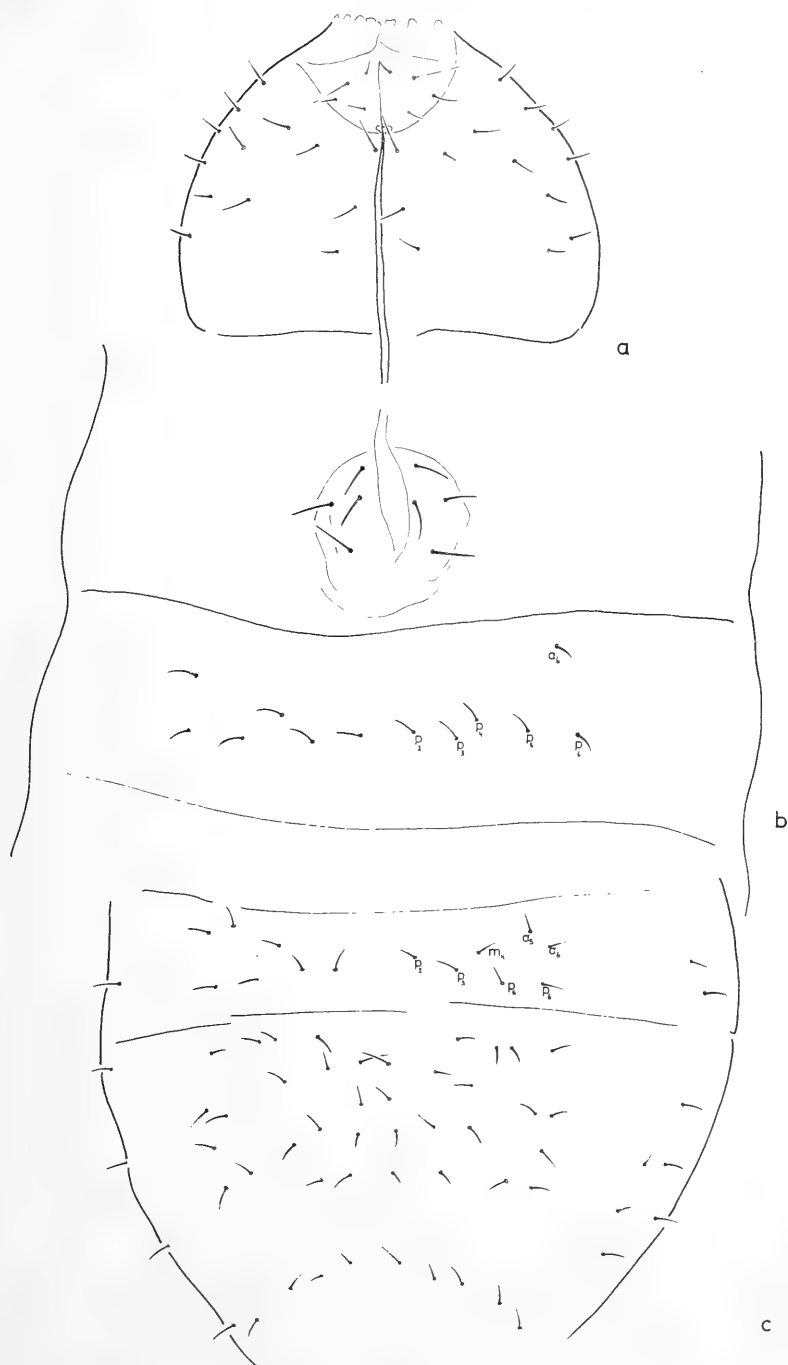


Fig. 8. *Acheroxenylla cretensis* n. sp. a, ventral chaetotaxy of head; b, ventral chaetotaxy of  $abd_{1-2}$ ; c, ventral chaetotaxy of  $abd_{3-4}$

Postantennal organ lacking. Only 2 + 2 small, widely separated ocelli.

Feet normal, short, unguiculus absent, unguis without any tooth, two dorsal tenent hairs (with one normal, short hair between them) very faintly clavate (Fig. 5f). Ventral tube with 4 + 4 setae (Fig. 8b).

Chaetotaxy. Cephalic chaetotaxy is interpreted along the lines indicated by Cassagnau (1974), who in essence restored the system of Yosii (1960). Rows p and c are complete, there is but one seta v, setae  $d_{1-3}$  and  $a_0$  are present, the sd row is very short, consisting of but two setae, allegedly  $sd_3$  and  $sd_5$ . The affinity with *Xenylla* is evident, only the sd row is still more reduced.  $Th_1$  with 3 + 3 setae.  $Th_{2-3}$  with  $a_1$ ,  $a_2$ ,  $a_{4-7}$ ,  $m_1$ ,  $m_3$ ,  $m_4$ , and  $m_7$ , and the p row complete:  $p_{1-6}$ . Seta  $p_4$  is ss. On  $th_3$ , moreover, a pair of setae  $m_5$  is present (Fig. 6).

Abd<sub>1-4</sub>: seta  $p_5$  is ss. Abd<sub>4</sub>: in frontal row only  $a_1$  and  $a_3$ , in median row only  $m_1$ , posterior row complete  $p_{1-5}$ . Abd<sub>5</sub>: only  $a_1$ ,  $p_{1-3}$  present;  $p_3$  = ss. Abd<sub>6</sub> with 3 + 3, anteriorly serrate setae (Fig. 7).

Ventral chaetotaxy: Head with  $a_1$ ,  $m_1$ , and  $p_1$  present,  $m_{2-3}$  lacking (Fig. 8a). All thoracal sternites and abd<sub>1</sub> without setae. Abd<sub>2</sub>:  $a_6$ ,  $p_1$ ,  $p_{3-6}$  (Fig. 8b). Abd<sub>3</sub>:  $a_{5-6}$ ,  $m_4$ ,  $p_1$ ,  $p_3$ ,  $p_{5-6}$ . It is not possible to analyse the setae on abd<sub>4</sub> (Fig. 8c).

Subcoxae 1-3 with 1, 2, 3 setae, respectively.

### ***Acherontiellina bougisi rhodia* (Ellis, 1974) n. comb. (Fig. 9 a, b)**

*Acherontiella bougisi rhodia* Ellis, 1974.

Material: sample 4: 8 ♀, 9 ♂, and 1 juv.; 6: 8 ♀ and 1 ♂; 7: 5 ♀ and 1 ♂; 9: 2 ♂ and 1 juv.; 10: 2 ♀; 11: 4 ♀, 1 ♂, and 1 juv.; 16: 2 ♀; 29: 4 ♀ and 1 ♂; 30: 13 ♀ and 6 ♂; 32: 2 ♀, 1 ♂, and 1 juv.; 33: 1 ♂ and 1 juv.; 34: 3 ♀ and 3 ♂.

Discussion. The present material is in good agreement with the two specimens from Rhodes on which I based the subspecies. The larger material now available permits me to add some supplementary details and to analyse some aspects of the variability.

The internal tooth at the unguis is usually clearly visible. Generally, though perhaps not in all specimens, the two tenent hairs are feebly clavate.

As I have already indicated, the dorsal chaetotaxy is identical to that of *bougisi bougisi*, discussed and illustrated by Thibaud (1967). However, some variability interferes with this agreement. In particular, seta  $a_0$  on the head is rather often lacking (in 27% of 60 observations). The row of setae sd, basically consisting of three setae  $sd_{3-5}$ , is reduced in some cases to two hairs  $sd_{4-5}$ . In 3% of the observations this reduction of sd occurred on only one side, in another 4% it occurred symmetrically ( $n = 61$ ). In one specimen seta v was lacking on both sides, and in 5% (3 cases) only unilaterally ( $n = 61$ ).

The ventral chaetotaxy can be summarized as follows. The head possesses  $a_1$ ,  $m_1$ , and  $m_3$  as well as generally a pair of setae  $p_1$ . In 16% seta  $p_1$  is lacking on one side, in 5% on both ( $n = 71$ ) (Fig. 9b). The thoracic sternites are without setae. The ventral tube has 4 + 4 setae as in *Xenylla*. Ventral chaetotaxy of abd<sub>2-3</sub> is very irregular, in abd<sub>2</sub>  $a_6$  is distinct, and there is a very unstable row p, consisting of 5 + 5 setae; either  $p_2$  or  $p_3$  is particularly strong and seems to have a sensory

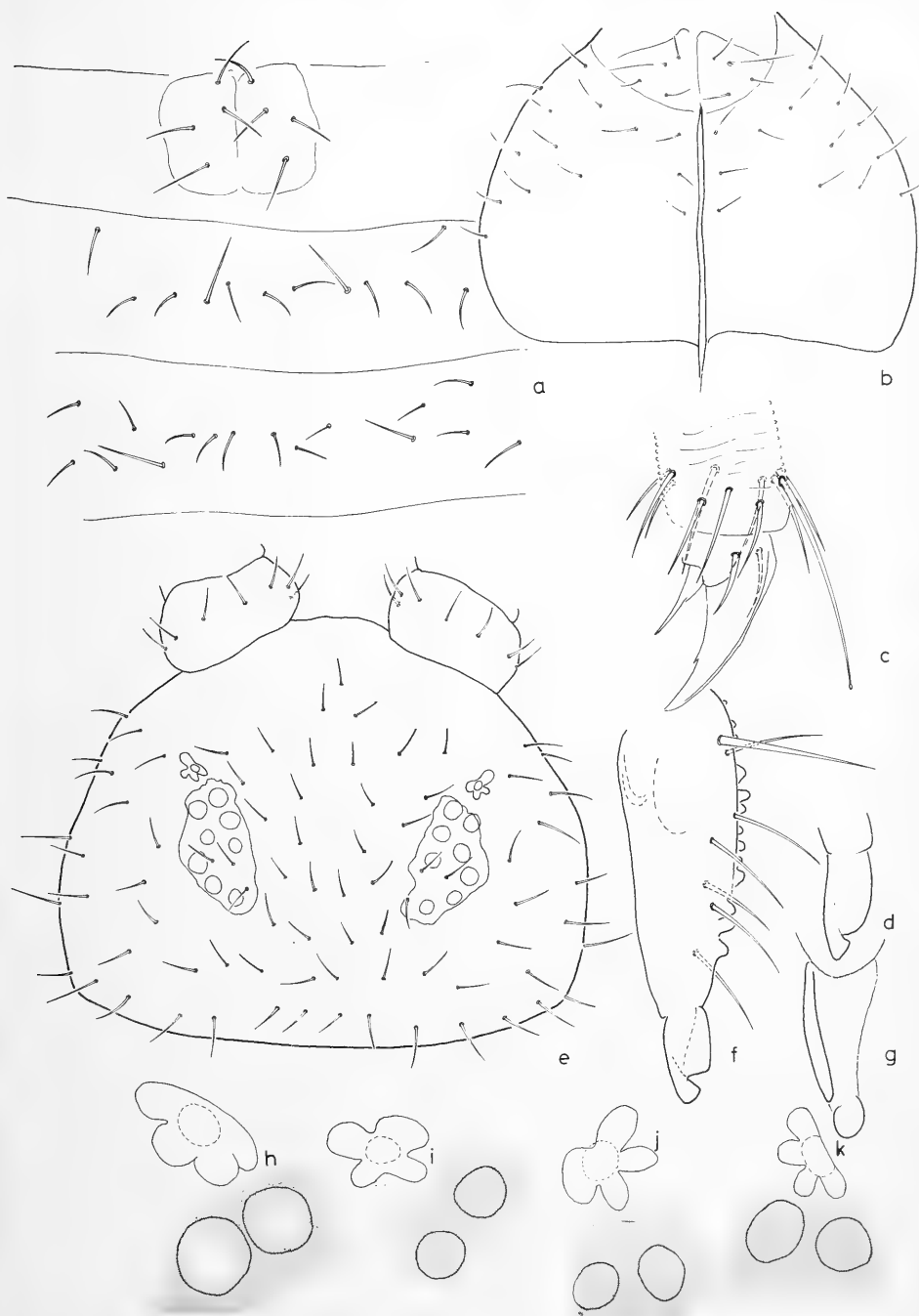


Fig. 9. *Acherontiellina bougisi rhodia* (Ellis). a, ventral chaetotaxy of  $\text{abd}_{1-3}$ ; b, ventral chaetotaxy of head. *Hypogastrura* cf. *gisini* Strenzke. c, unguis  $\text{P}_3$ ; d, mucro exterior; e, dorsal cephalic chaetotaxy; f, lateral aspect of mucrodens; g, posterior face of mucro; h, i, j, k, postantennal organs

function (Fig. 9a). In abd<sub>3</sub> setae a<sub>5-6</sub> are evident, but it was not possible to discern a row m or p, nor was the position of a pair of sensory hairs sufficiently stable to establish a fixed scheme.

By transferring *bougisi* to the genus *Acherontiellina*, I adopt the classification proposed by Djanaschvili (1971a, b), which is assimilated into the key to the genera of the *Xenylla* group (p. 238).

### *Xenylla maritima* Tullberg, 1869

Material: sample 3: 3 ♀, 1 ♂, and 4 juv.; 50: 17 ♀ and 4 ♂ + 8 ex. in alcohol.

*Xenylla maritima* is a well-known species, reported from all European countries and, with varying certainty, elsewhere. The material agrees completely with the detailed chaetotactical description by Da Gama (1969).

### *Ceratophysella succinea* (Gisin, 1949) (bona species?)

Material: sample 23: 2 juv.; 24: 1 ♂; 26: 3 ♀ and 9 juv.; 32: 1 ♀ and 1 juv.; 37: 1 ♀; 41: 2 ♂ and 7 juv.; 44: 2 juv.; 48: 2 ♀, 4 ♂, and 8 juv. + 15 ex. in alcohol; 49: 4 ♀, 1 ♂, and 1 juv.

Discussion. The material is easily placed in species group A<sub>1</sub>, the *denticulata* group, of Bourgeois & Cassagnau (1972): on abd<sub>4</sub> are present: a<sub>1</sub> and a<sub>3</sub>, m<sub>1</sub> and m<sub>4</sub>, and p<sub>1-3</sub>, where p<sub>2</sub> and p<sub>4</sub> are macrochaetae and p<sub>3</sub> is ss. Within this group, the material could be attributed to *C. engadinensis* (Gisin, 1949), characterized by having 7+7 setae on the dentes and normal anal spines; or alternatively to *C. succinea*, which was differentiated on the basis of its having only 6+6 setae on the dentes and strong, yellow anal spines.

Since Cassagnau and his collaborators' work on ecomorphosis and epitocal processes in Hypogastruridae has shown that characters derived from integumentary details other than chaetotaxy are unstable and of limited use, the last-mentioned characters must be approached with caution. However, the number of dental setae was not more informative in the present material. In fact, all gradations between 5+5 and 7+7 setae were encountered: 5+5: 1 ×; 5+?: 1 ×; 5+6: 2 ×; 5+7: 1 ×; 6+6: 12 ×; 6+?: 2 ×; 7+6: 10 ×; 7+7: 12 ×; 7+?: 4 ×. It was not possible to correlate the number of dental setae with the size of the specimens or their sexual maturity. For 41 observations, I obtained a correlation coefficient of  $r = 0.255$ ; for a 5% significance, a value of 0.321 would be required. In sample 26, no specimen with more than 6 setae per dens were found, but in the other, larger samples all values occurred.

Evidently, some doubt concerning the separation of *succinea* and *engadinensis* is warranted. However, in this genus, perhaps more than in any other collembolan group, the results of rearing experiments must be decisive and, basing myself on material from a different faunal region, I do not dare to synonymize two species described after Swiss material. I prefer to identify my Greek material with *succinea*, because the specimens generally have honey-coloured anal spines, which are indeed rather long, and moreover because *succinea* has already been mentioned from Greece (Evvia) by Bourgeois & Cassagnau (1972).

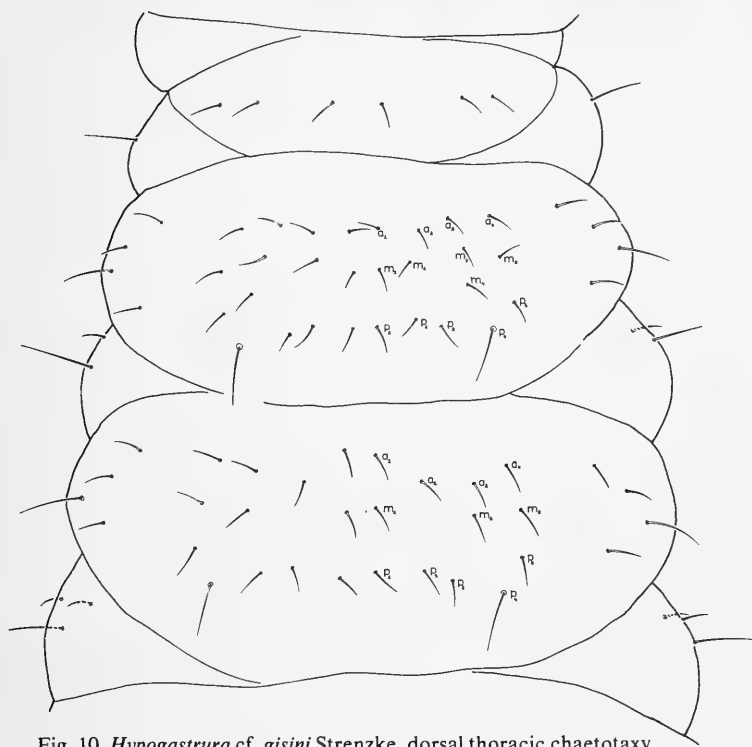


Fig. 10. *Hypogastrura* cf. *gisini* Strenzke. dorsal thoracic chaetotaxy

Seta  $a'_2$  on abd<sub>5</sub> (i.e., the seta differentiating *C. denticulata* from *engadinensis*), which Bourgeois & Cassagnau found in 33% of their adult specimens of *succinea* from Evvia, only occurred sporadically in my material; it was found in two immatures from sample 26, and in a female from 49, each time on one side only.

*C. succinea* has been recorded from Spitsbergen, Jan Mayen, Germany, Switzerland, Austria, the USSR, Bulgaria, and Yugoslavia. There are records of *engadinensis* from Switzerland, Austria, Poland, France, and Spain.

#### ***Ceratophysella gibbosa* (Bagnall, 1940)**

*Hypogastrura occidentalis* Gisin, 1958.

Material: sample 32: 1 ♀; 34: 1 juv.; 41: 8 juv.; 42: 1 juv.

This species, described from the British Isles, is, according to Yosii (1966a) "almost cosmopolitan". *H. occidentalis* was described from Madeira.

#### ***Ceratophysella armata* (Nicolet, 1841)**

Material: sample 35: 4 juv.; 36: 1 juv.; 43: 5 juv.

The species has been recorded from most European countries. It is difficult to assess the distribution of the species, because the classical species *armata* has been subdivided during recent decades.

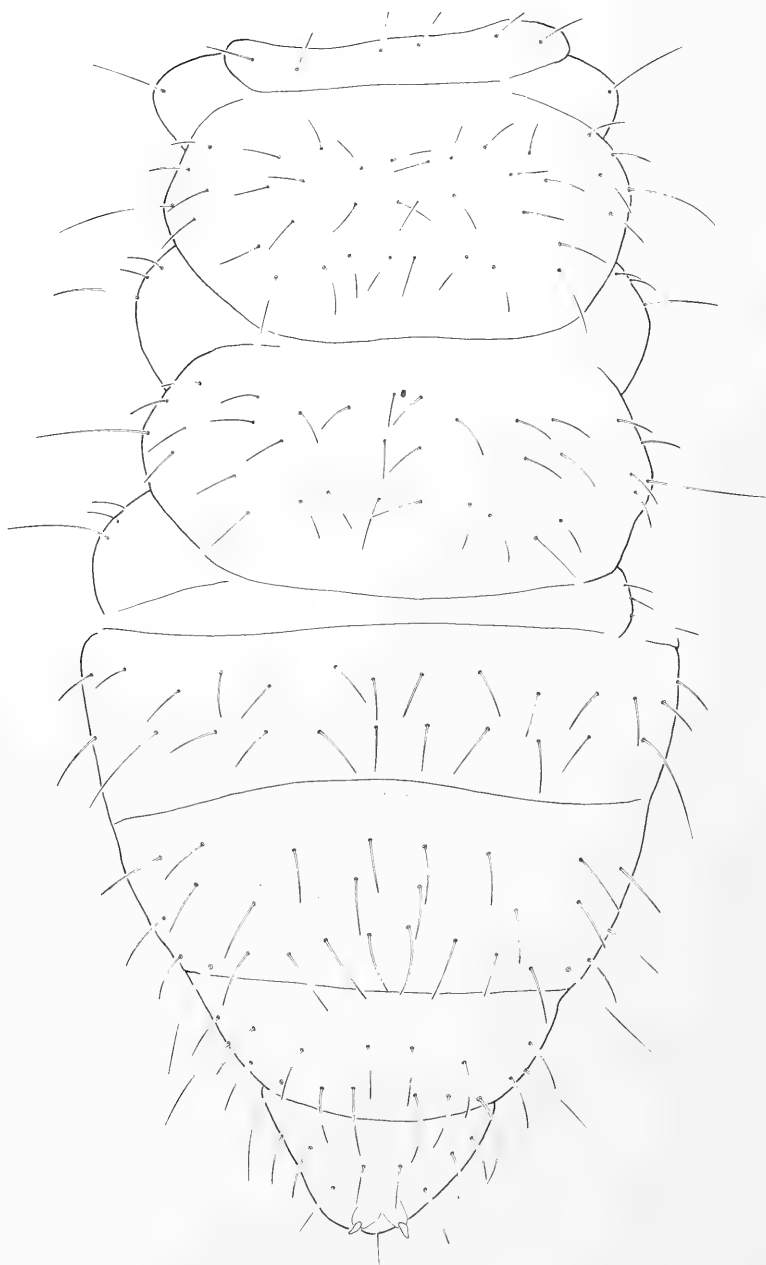


Fig. 11. *Hypogastrura tethyca* n. sp. dorsal chaetotaxy of thorax and abd<sub>3-6</sub>



**Hypogastrura cf. *gisini* Strenzke, 1955 (Fig. 9 c-k, 10, 12 a-e)**

Material: sample 3: 1 ♀; 10: 10 ♀, 2 ♂, and 1 juv.; 11: 1 ♂; 13: 1 ♂ and 1 juv.; 18: 2 ♀ and 4 ♂; 23: 12 ♀, 4 ♂, and 3 juv.; 26: 2 ♀; 27: 1 ♂; 32: 4 ♀ and 1 ♂; 33: 8 ♀, 5 ♂, and 1 juv.; 36: 5 ♀.

Description. Total length 0.9-1.1 mm. Sparse greyish-blue pigment, scattered lightly, even eye patches not completely obscured. Integument moderately and rather evenly granulate. Posterior face of dens not much more strongly granulated. Anal spines short (about 6-7  $\mu$ , or  $\frac{1}{2}$ - $\frac{1}{3}$  unguis  $P_3$ ), curved, on papillae which are as high and only free at the base (Fig. 12a). Eyes 8+8.

Antennae about as long as diameter of head, with retractile apical papilla, 1 inner and 3 outer slightly swollen and curved sense hairs. Antennal organ III normal. Postantennal organ small, about two times as large as next ocellus, with 4 (occasionally 3) short and wide lobes, about as large as central part, broadly attached. Accessory tubercle often invisible (Fig. 9h-k).

Tibiotarsi with 1, 1, 1, weakly clavate tenent hairs. Unguis with small inner tooth; no lateral teeth visible; unguiculus about half as long as unguis, with a very weak basal lamella, tapering apically (Fig. 9 c). Ventral tube with 4+4 setae; retinaculum with 3+3 teeth.

Dens with 7+7 setae, posterior face not strongly granulated, about 2.5-3 times mucro (Fig. 9f). Mucro of *assimilis*-type, with globular apical tooth and a rather high outer lamella (Fig. 9d, g).

Chaetotaxy. All hairs comparatively long, smooth. No differentiation into micro- and macrochaetae. Chaetotaxy of head complete (row p, c,  $d_{1-5}$ ,  $sd_{1-5}$ ,  $a_0$ ,  $oc_{1-3}$ ,  $v_{1-2}$ ). Thoracic chaetotaxy:  $th_1$ : 3+3 setae;  $th_2$ :  $a_{1-4}$ ,  $m_{1-5}$ ,  $p_{1-5}$ ,  $p_4=ss$ .  $Th_3$  is as  $th_2$ , except that  $m_2$  and  $m_4$  are missing (Fig. 10). Subcoxae 1, 2, 3.

Abdomen $_{1-3}$  with two rows. Abd $_4$  with complete a and p rows, and ss in  $p_5$ . The m row is represented by  $m_1$ ,  $m_3$ , and  $m_5$ . However, irregularities occur rather frequently, especially in  $m_3$ , but even the p row may be affected, Abd $_5$  with  $a_{1-3}$  and  $p_{1-3}$  ( $p_3=ss$ ), and also an m row normally composed of 3+3 setae. Here as well, irregularities occur rather frequently, and affect especially the presence of  $m_1$  (Fig. 12b-d).

Ventral chaetotaxy of head complete ( $a_1$ ,  $m_1$ ,  $m_2$ ,  $p_1$ ).  $Th_{1-3}$  without setae.

Discussion. The Greek material comes reasonably close to *gisini* Strenzke, which has been described from sandy beaches along the German North Sea and Baltic coasts. There is only one striking difference: *gisini* has an unguiculus  $\frac{1}{4}$ - $\frac{1}{3}$  the length of the unguis, whereas in the Cretan material it is much longer. It is unfortunate that the chaetotaxy of *gisini* is not known; I have not been able to examine type material.

The material also shows a striking resemblance to *H. capitata* Cassagnau & Delamare Deboutteville, 1955, from the Lebanon. This species differs in possessing a strong tooth at the unguis, an unguiculus with a distinct lamella, a dens with 6 setae and a proportionally shorter mucro, and feebly clavate body setae. Since not all of these characters are very decisive, a redescription of *capitata* is necessary.

Another species, *H. christianseni* Yosii, 1960, from the United States, could

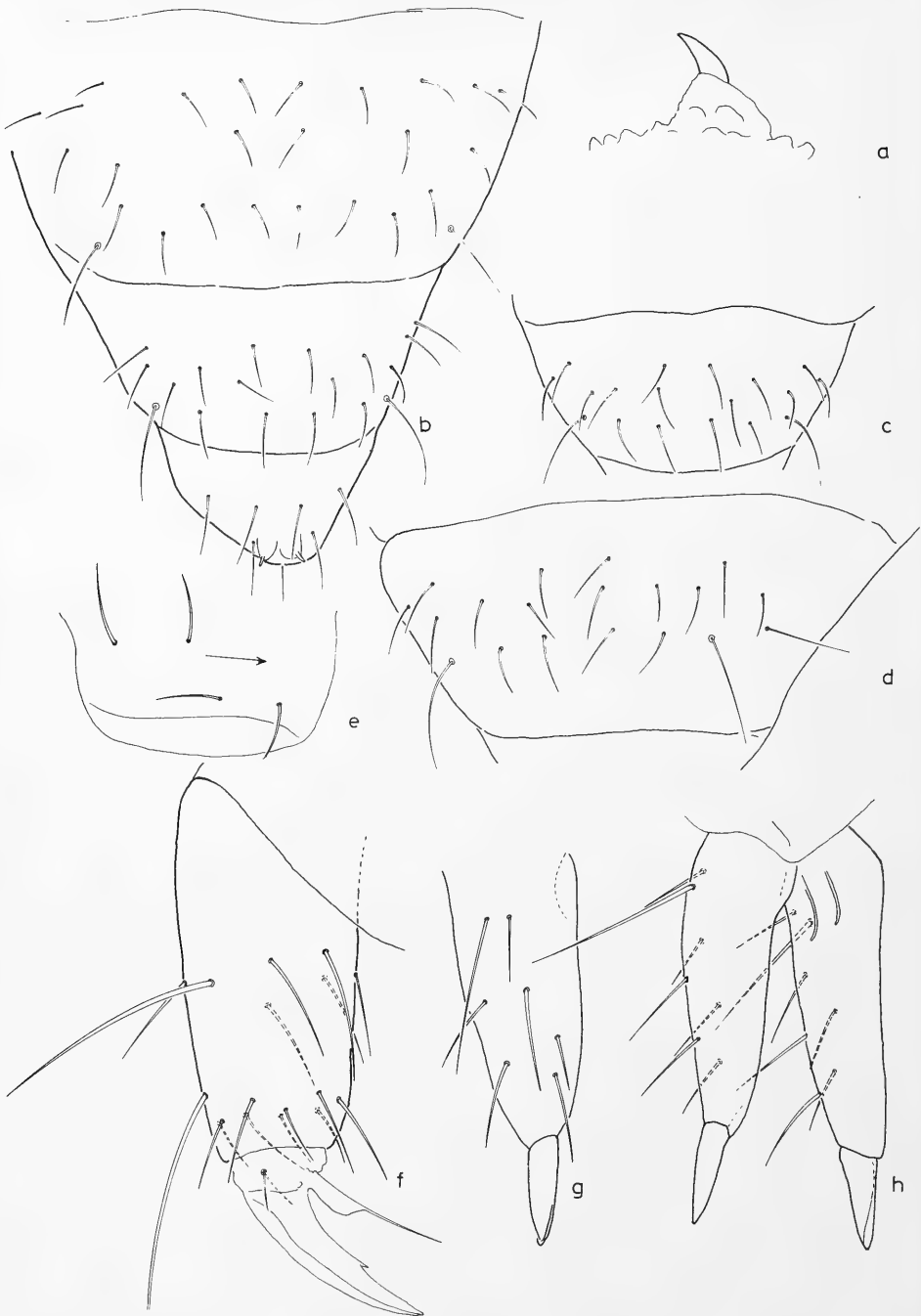


Fig. 12. *Hypogastrura* cf. *gisini* Strenzke. a, anal spine in lateral view; b, dorsal chaetotaxy of abd<sub>4-6</sub>; c, d, dorsal chaetotaxy of abd<sub>5</sub> of two different specimens. *Hypogastrura tethyca* n. sp. e, ventral tube in lateral view; f, tibiotarsus and claw of P<sub>3</sub>; g, posterior face of dens; h, oblique view of mucrodentes of another specimen

according to its description be conspecific with the present material. Upon my request, Professor Yosii kindly gave me the type-series of this species. A study of this material revealed seta  $m_2$  to be present on  $th_2$ , contrary to the original description. At the time of that publication, the improbability of the absence of this hair was of course not yet known. This finding seemed to remove the last point of difference, but on the same occasion the number of retinacular teeth, stated incorrectly to be 3+3, proved in reality to be 4+4. This, as Yosii remarks, brings *christianseni* into close proximity with *assimilis* Krausbauer, 1898; it remains distinct because it bears an  $m$  row on  $abd_3$ .

### **Hypogastrura manubrialis** (Tullberg, 1869)

Material: sample 23: 2 ♀, 3 ♂, and 3 juv.; 31: 1 ♂; 32: 6 ♀, 4 ♂, and 1 juv.; 41: 5 ♀, 2 ♂, and 1 juv.; 42: 3 ♂; 47: 1 ♀.

Discussion. *H. manubrialis* is easily distinguished from the foregoing species by the larger number of antennal sense hairs, the different structure of the PAO (the lateral tubercles are located above their insertion on the central tubercle, and thus seem mutually unconnected), the retinaculum with 4+4 (in a few instances 3+4) teeth, the slender acute mucro, the coarsely papillate posterior face of dens, and the small almost straight anal spines. Bourgeois & Cassagnau's (1972) observation that  $m_2$  is missing in  $th_2$  is confirmed.

The species has been recorded from most European countries, and also from most continents.

### **Hypogastrura tethyca** n. sp. (Fig. 11, 12 e-h, 13)

Material: sample 10: 1 ♀; 30: 3 ♀, 4 ♂, and 1 juv.; 31: 10 ♀ and 8 ♂; 32: 2 ♀; 37: 1 ♂ and 1 juv.; 43: 1 ♀ and 1 ♂; 44: 5 ♀, 12 ♂, and 6 juv.; 45: 1 ♂ and 1 juv. Holotype is a ♂ from sample 44.

Description. Length of largest specimens 1.9-2.0 mm. Bluish-grey pigment forms irregular mottling, and an irregular panther-pattern all over the body, but less pronounced on ventral parts and extremities. Dens in particular almost without pigment.

Integument finely and regularly granulate.

Antennae about 0.9 times head diagonal. Ant<sub>4</sub> with retractile, entire papilla, 3 outer and 1 inner slender, strongly curved sense hairs, ventrally about 20 short stiff apically truncate hairs form a kind of sensory rasp. Ant<sub>3</sub> with 2 short curved sensillae and 2 long and rather slender sense hairs (Fig. 13 e).

Eyes 8+8 on intensely pigmented eye patch. Postantennal organ distinctly wider than nearest ocellus, consisting of 4 bladders, the anterior two the longest. Accessory boss present (Fig. 13 f, g). Rim of labrum with 4 flat protuberances (Fig. 13 d); labral setae 4/5, 5, 4.

Tibiotarsi with 1, 1, 1 long, feebly but distinctly clavate tenent hairs. Unguis with distinct internal tooth, lateral teeth absent or extremely small. Unguiculus with large basal lamella and a filament about 2/3 internal length of unguis (Fig. 12 f).

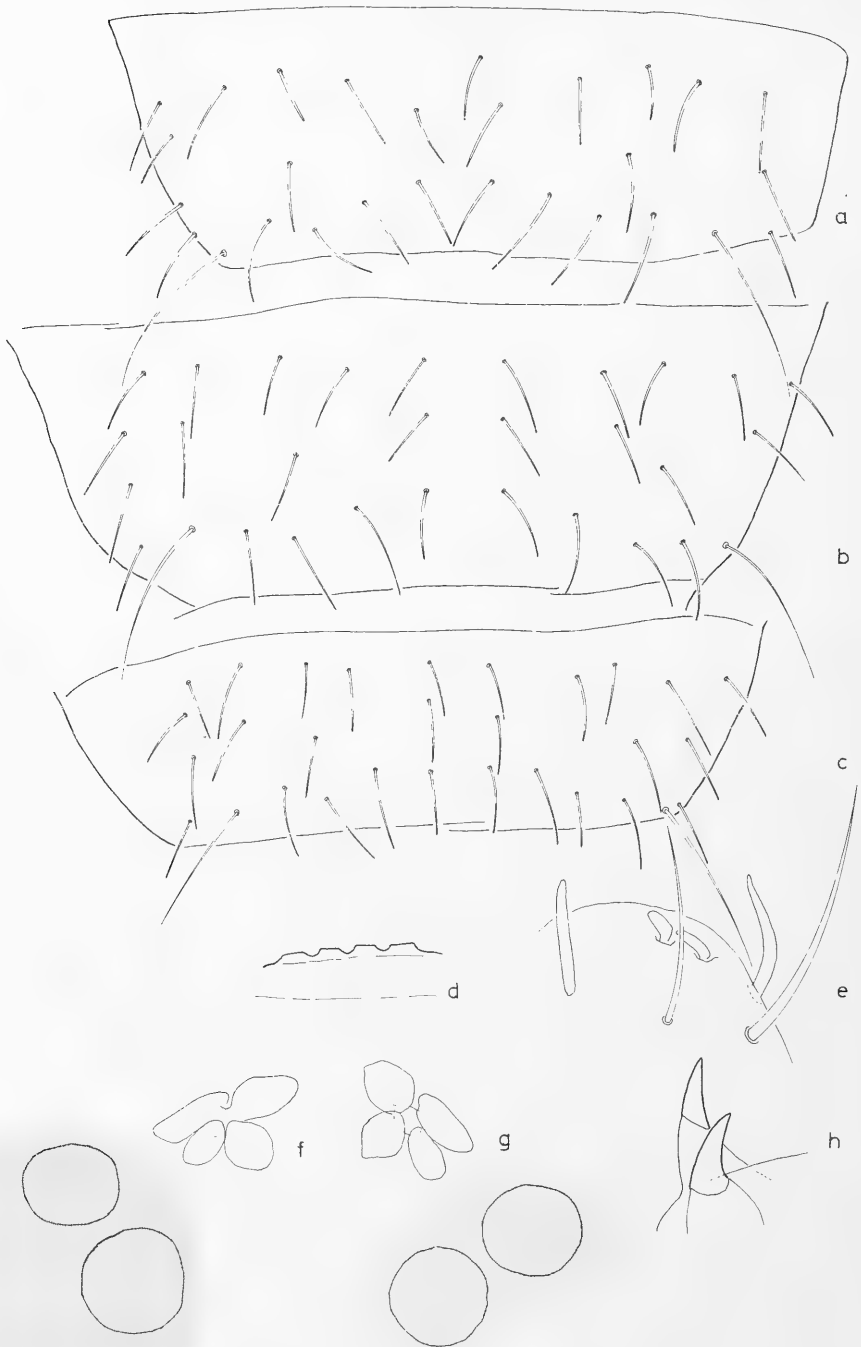


Fig. 13. *Hypogastrura tethyca* n. sp. a, b, c, dorsal chaetotaxy of  $\text{abd}_4$  of three specimens; d, labral margin seen from ventral; e, antennal organ III; f, g, postantennal organs of two specimens; h, anal spines in oblique view

Ventral tube with 4+4 setae (Fig. 12 e). Retinaculum with 4+4 teeth, rarely 3+4.

Dens 100  $\mu$ , mucro about 36  $\mu$ . Dens with 7 setae. Posterior face of dens finely granulated. Mucro elongate, with only very weak inner and outer lamellae (Fig. 12 g, h).

Anal spines well developed, slightly curved, ca. 19  $\mu$ , on (almost touching) anal papillae of 22  $\mu$  (Fig. 13 h).

Chaetotaxy composed of strong, comparatively stiff, at their anterior face rugose to slightly serrate, setae. The setae are all alike, except that in posterior direction the dorsal setae become stronger. Setae sensuales easily recognized by their length and structure.

Cephalic chaetotaxy with complete rows p and c,  $v=2$ , d and sd = 5, oc = 3,  $a_0$  present. Th<sub>1</sub> 3+3 setae. Th<sub>2</sub> complete, p<sub>4</sub> = ss; th<sub>3</sub> as th<sub>2</sub> but m<sub>2</sub> and m<sub>4</sub> missing (Fig. 11). Abd<sub>1-3</sub> with two rows of setae. Abd<sub>4</sub> difficult to interpret because of many irregularities (Fig. 13 a-c). The p row is always complete. Between setae p<sub>5</sub> (ss) the a row normally shows only 3+3 setae, but not infrequently 3+4 or 4+4; the m row consists of 3+3 or 2+2 setae. Abd<sub>5</sub> with 2+2 setae in the a row between p<sub>3</sub>-p<sub>3</sub>, and never with an m row (Fig. 11).

Ventral chaetotaxy of head with a<sub>1</sub>, m<sub>1-3</sub>, p<sub>1</sub>. Thorax ventrally without setae.

Diagnosis. I find it very difficult to give this species a place in the genus. Using the key given by Gisin (1960) one arrives blindly at *Hypogastrura sahlbergi* (Reuter, 1895) or *H. capitata* Cassagnau & Delamare, 1955. The new species differs from the former by the different shape of the anal spines and their papillae, by the structure of the setae — short, slender, and pointed in *sahlbergi*, long stiff bristles in *tethyca* — and above all by having not 7-8 setae at each side of the ventral tube, but the normal number 4+4. *H. capitata*, seemingly more closely related to *H. gisini*, has 3+3 teeth on the retinaculum, clavate body setae, and a different mucro.

The strong basal lamella of the unguiculus is reminiscent of such species as *tullbergi*, *viatica*, etc., but these have more than 1 clavate tenent hair on the tibiotarsi. *H. monticola* Stach, 1946, has the single tenent hair not clavate, very short anal spines, and a "spoon-like" mucro. *H. packardi* (Folsom, 1902) has capitate body setae, an extremely heavy clavate tenent hair, and, even in the forma *dentata*, too short an unguiculus; according to Bourgeois & Cassagnau, the chaetotaxy is differentiated into micro- and macrochaetae. *H. aterrima* Yosii, 1972, from Japan, has 3+3 teeth on the retinaculum and a strong differentiation into micro- and macrochaetae. *H. paradoxa* Yosii, 1965, also from Japan, seems in some respects close to *tethyca*: 1 clavate tenent hair on tibiotarsus, same shape of anal spines and claw, etc.; however, that species forms a link with *Ceratophysella* in having a small exsertile sac between ant<sub>3</sub> and ant<sub>4</sub> as well as a peculiar chaetotaxy, an m row being fully present on abd<sub>4</sub> and abd<sub>5</sub>. In *H. theeli* (Tullberg, 1876) s. Yosii, 1972 = *H. trybomi* (Schött, 1893) s. Hammer, 1953, the tenent hair is not clavate. *H. macrotuberculata* Hammer, 1953, has a highly divergent mucro with a high lamella.

The species is dedicated to Tethys, goddess of the sea, who embodies at the

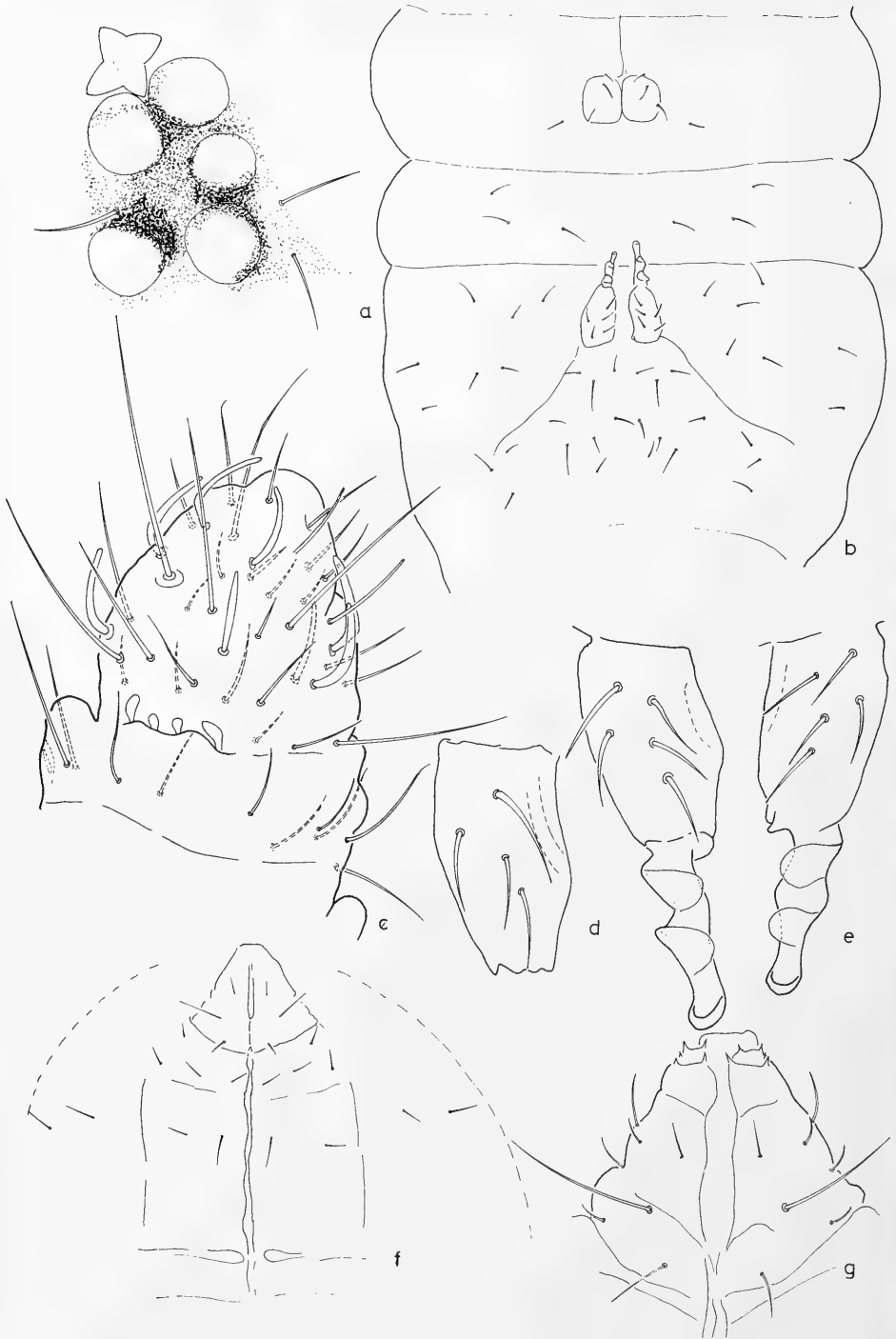


Fig. 14. *Odontella nana orientalis* n. ssp. a, eye patch and postantennal organ; b, ventral chaetotaxy of abd<sub>1-4</sub>; c, ant<sub>3-4</sub>; d, atypical dens; e, typical mucrodentes; f, ventral chaetotaxy of head; g, mouth cone

same time the very sea that shaped the present zoogeographical pattern of the Greek Collembola.

### ***Hypogastrura vernalis* (Carl, 1901)**

Material: sample 10: 4♀ and 1♂ ; 17: 2♀ and 1♂ .

Recorded from Scandinavia to the Mediterranean and from the British Isles to Poland. Along the Mediterranean it has been found from the Iberian peninsula to Yugoslavia.

## NEANURIDAE

### ***Odontella nana orientalis* n. ssp. (Fig. 14, 15, 16 a-b)**

Material: sample 29: 1♀ and 7♂ ; holotype is a ♂ .

Description. Mean length of the males is 0.60 mm ( $s = 0.016$ ,  $s_{\bar{x}} = 0.006$  mm), the single female measures 0.89 mm; statistically, this difference is strongly significant ( $t = 16.353$ ,  $df = 6$ ,  $P < 0.001$ ).

Greyish-blue pigment sparse on dorsal parts of body and head and, even more so, on feet and furca. Eye patch strongly pigmented. Integument with primary granules arranged in a tetragonal lattice. The skin is strongly folded in an irregular way. Habitus normal for the genus, with very short conical antennae.

Mouth-parts normal for the genus (Fig. 14 g), labium with some short and 1 + 1 long hairs. Ocelli 5 + 5, c somewhat smaller than the others. Postantennal organ a pretty four-pointed star, perfectly symmetrical (Fig. 14 a). Ant<sub>3</sub> with a sensilla at outer face. Ant. organ III two short cones, and laterally from them two bent, swollen claviform clubs. Ant<sub>4</sub> with 8 sense hairs and an apical cupola (Fig. 14 c).

Claw slender, with strong basal tooth on inner lamella, and a pair of teeth basally on lateral lamellae. No unguiculus. No clavate tenent hair (Fig. 16 b).

Ventral tube with 3 + 3 setae. Retinaculum tridentate. Dentes with 5 + 5 setae (Fig. 14 e) but one specimen had 4 + 5 (Fig. 14 d). Mucro typical. Male genital tubercle small, with 10 setae. Female genital cleft guarded by no more than 3 setae. Ventral flaps of anal segment with some remarkably strong setae. Anal spines very short and conical, on very low papillae. The anal spines are often present on one side only, and in one instance one was cleft. The presence of the spines is evidently an unstable character, although their shape is very constant.

Chaetotaxy (Fig. 15), composed of fine, rather short, smooth setae which are never clubbed. Cephalic chaetotaxy rather reduced: present are  $p_{1-4}$ ,  $c_3$ , ( $p_1$  may sometimes seem to be  $c_1$  as well),  $d_1$ ,  $d_{3-5}$ ,  $sd_{3-5}$ ,  $oc_{1-3}$ ;  $a_0$  is absent.  $Th_1$  with the peculiar number of 4 + 4 setae.  $Th_{2-3}$  identical, with  $a_1$ ,  $a_{3-5}$  (other setae of a row difficult to interpret, see Fig. 15),  $m_1$ ,  $m_4$ ,  $p_{1-2}$ ,  $p_4 = ss$ ,  $p_5$ . Cassagnau (1974) gives a somewhat different interpretation of the thorax of *O. nana* Cassagnau, 1954. According to this author,  $a_2$  is present in  $th_2$ , but absent in  $th_3$ . Some individuals on a slide with specimens of *nana*, preserved in the collection of the Laboratoire d'Ecologie générale, Brunoy, unfortunately without indication of locality, showed a much more median position of the hair on  $th_2$  labelled by me as  $a_3$ , i.e., almost

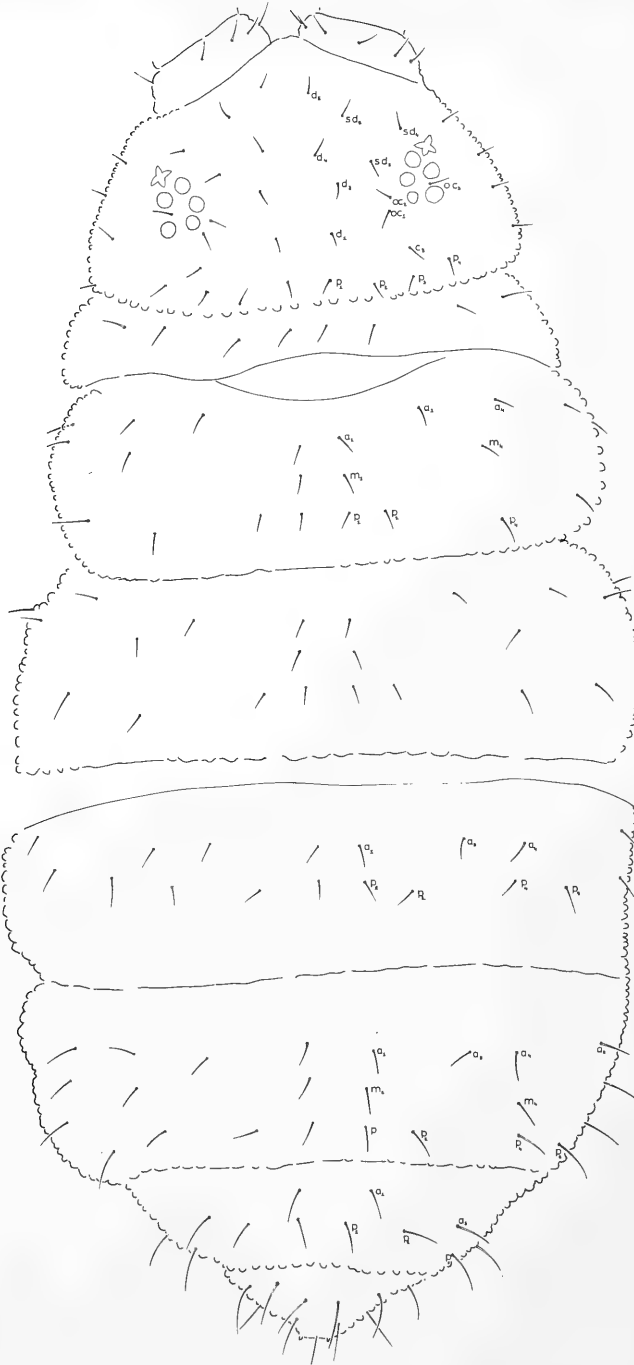


Fig. 15. *Odontella nana orientalis* n. ssp. dorsal chaetotaxy



anterior to  $p_2$ . Otherwise, they seemed identical to the Greek specimens in chaetotaxy.

Abd<sub>1-3</sub> alike, with two rows, consisting of  $a_1$ ,  $a_{3-4}$ ,  $p_{1-2}$ ,  $p_{4-5}$ ;  $p_5 = ss$ . Abd<sub>4</sub> as abd<sub>1-3</sub> but with the insertion of an  $m$  row with  $m_1$  and  $m_4$ . Abd<sub>5</sub> with  $a_1$ ,  $a_3$ ,  $p_{1-3}$ ;  $p_3 = ss$ .

Ventral chaetotaxy of head with  $a_{1-3}$ ,  $m_{1-2}$ , no posterior setae (Fig. 14 f). Thoracic sternites without setae. Abd<sub>1</sub> with 1 + 1 setae near the ventral tube. Abd<sub>2</sub> with 2 + 2 setae in the posterior, and 1 + 1 in the anterior row. Abd<sub>4</sub> and the manubrium with a complicated array of setae (Fig. 16 b).

Discussion. Judging by the shape of the postantennal organ, the comparatively large number of sense hairs on ant<sub>4</sub>, and the presence of anal spines, the Cretan material belongs in the group of *O. stachi* Denis, 1947, described after one specimen from Burgundy, *O. nana* Cassagnau, 1954, described after a single specimen from the Pyrenees, and *O. vallvidrerensis* Selga, 1966, proposed for a richer material from NE Spain. It differs from *vallvidrerensis* in having 5 + 5 instead of 4 + 4 setae on the dentes, and from *stachi* in having a distinct lateral tooth on the unguis. It differs from all three by the very low, blunt anal spines, and above all the absence of the unguiculus. The latter character relates the present material to *O. sublamellifera* Denis, 1948, from Vietnam, but that species lacks the lateral teeth on the unguis and has a somewhat different, smaller, postantennal organ. In all other body characters it agrees closely with *O. nana*, and I prefer not to exaggerate the importance of the differences by making another new species.

If I may take the slide from Brunoy as a reference for *nana* s. str., another difference would be the absence of seta  $m_4$  on abd<sub>4</sub> in *nana nana*.

### **Xenyllodes minitaurus** n. sp. (Fig. 16 c-e, 17, 18, 19 a-d)

Material: sample 30: 1♂; 36: 1♀ and 1♂ (holotype).

Description. Total length of the only female 0.7 mm; the males are 0.5 and 0.6 mm. Habitus slender, strongly resembling that of a *Mesaphorura*. Basal skin reticulation in a normal, hexagonal lattice (very different from the quadrangular lattice in *Odontella*); skin folded in high conical papillae, which are absent only on the feet and furca. No pigment, but below each eye there is a small aggregation of colourless granules.

Ant<sub>3</sub> with small sensilla in external face. Ant. org. III with two small curved sensillae, and between them two almost imperceptible sense rods (Fig. 18 d). Ant<sub>4</sub> with retractile end bulb, and 6 swollen sense hairs. Hairs at ventral face mainly with a blunt apex (Fig. 16 d).

Eyes 2 + 2, separated by roughly their own diameter. Postantennal organ broadly and a bit irregularly triangular, sunken below the integument in a cavity communicating with the surface via a triangular fissure (Fig. 19 a, b). Mouth parts not studied. Mouth cone typical (Fig. 18 c). Tibiotarsi with some long hairs, which are possibly finely clavate (Fig. 19 d). Unguis strongly curved, without lateral or internal teeth. Unguiculus present, needle-shaped (Fig. 19 c).

Ventral tube with 3 + 3 setae.

Retinaculum bidentate. Manubrium with 2 + 2 setae; dentes almost quadrangu-

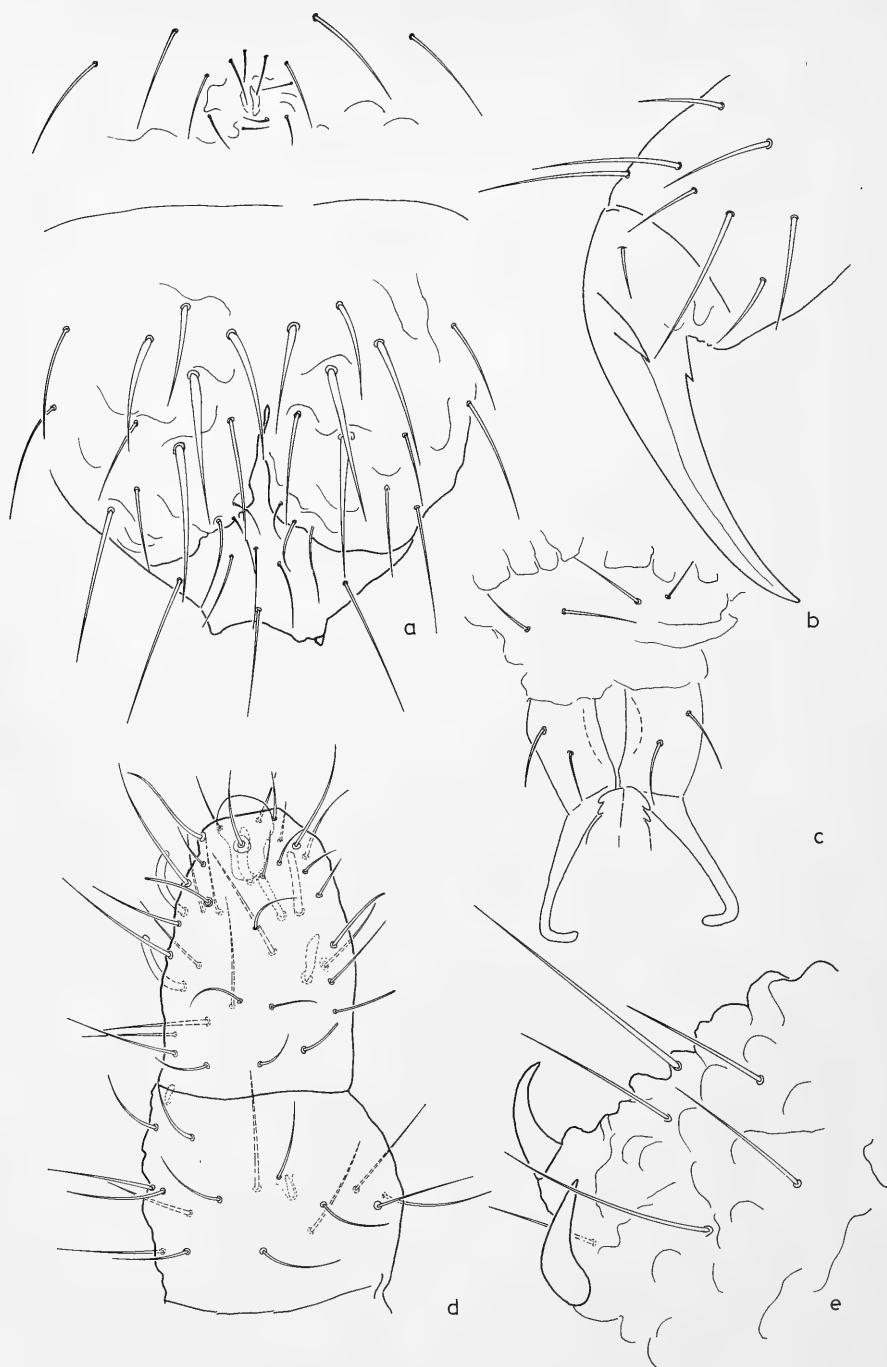


Fig. 16. *Odontella nana orientalis* n. ssp. a, ventral chaetotaxy of genital and anal areas; b, claw of  $P_2$ . *Xenyllodes minitaurus* n. sp. c, furca and retinaculum; d, ant<sub>3-4</sub>; e, anal spines

lar, smooth, with 2 + 2 setae. Mucro exceedingly long and crook-shaped (Fig. 16 c). Male genital papilla with about 11 setae; female genital orifice with 3 + 3 setae (Fig. 18 a). Two anal spines present, strong and curved, roughly 1.5 times unguis (Fig. 16 e).

Chaetotaxy composed of fine, smooth setae, nowhere differentiated (Fig. 17). Head lacking seta  $a_0$ , with setae  $p_{2-4}$ ,  $c_1$ ,  $c_{3-4}$ ,  $d_1$ ,  $d_{3-5}$ ,  $sd_{3-5}$ ,  $oc_{2-3}$ . As in *Odontella*,  $th_1$  has 4 + 4 setae. Chaetotaxy of  $th_2$  and  $th_3$  similar:  $a_{1-3}$ ,  $m_1$ ,  $m_3$ ,  $p_{1-2}$ ,  $p_{3-4}$ . It is not possible to recognize a seta sensuality in  $p_4$ .  $Abd_{1-3}$  with  $a_1$ ;  $a_{3-5}$ ,  $p_{1-5}$ .  $Abd_4$  lacks a

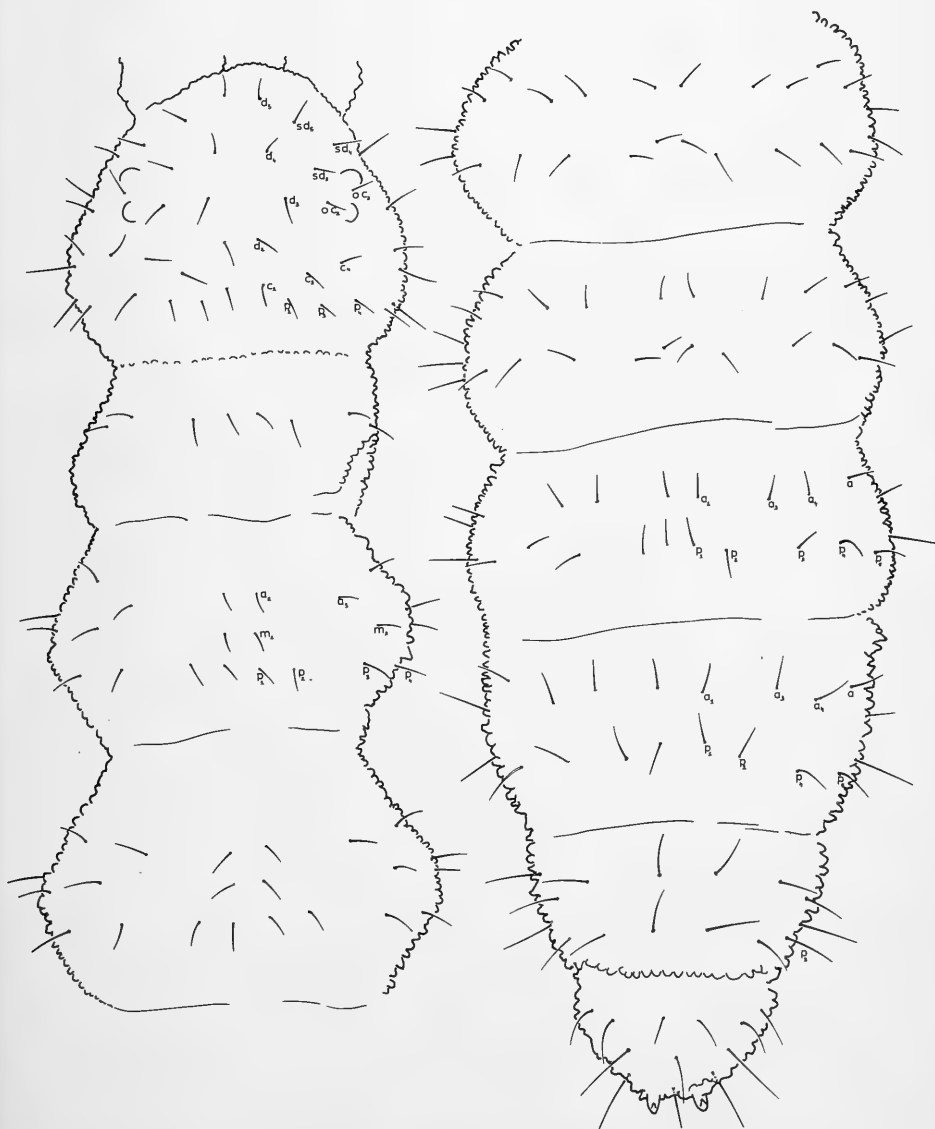


Fig. 17. *Xenyllodes minitaurus* n. sp., dorsal chaetotaxy

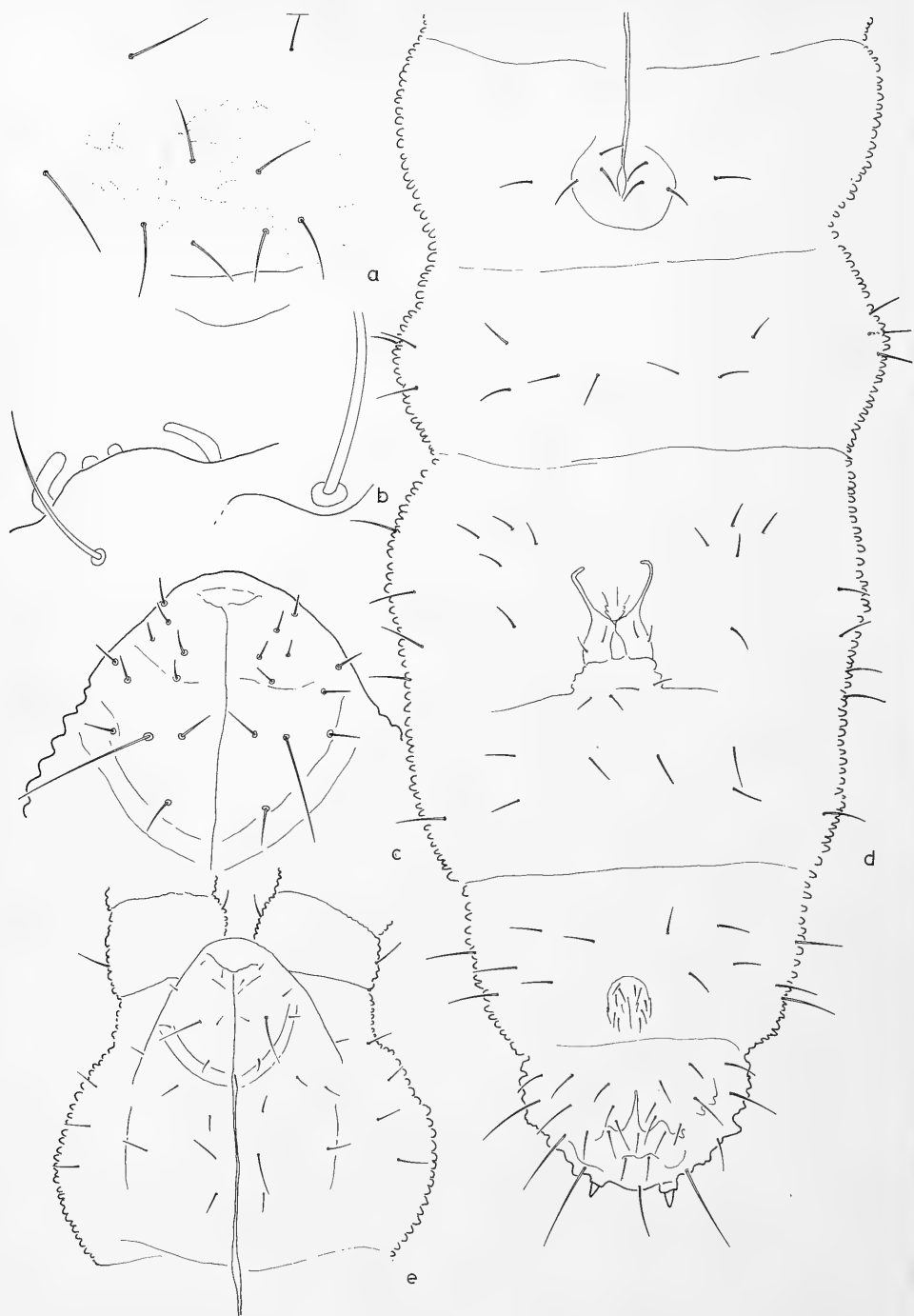


Fig. 18. *Xenyllodes minitaurus* n. sp. a, female genital orifice; b, antennal organ III; c, mouth cone; d, ventral chaetotaxy of abd<sub>1-6</sub>; e, ventral chaetotaxy of head

row m, and only has  $a_1$ ,  $a_{3-5}$ ,  $p_{1-2}$ ,  $p_{4-5}$ . Abd<sub>5</sub> with  $a_{1-3}$ ,  $p_{1-3}$ . Seta sensuality is, as usual,  $p_5$  in abd<sub>1-4</sub> and  $p_3$  in abd<sub>5</sub>. Abd<sub>6</sub> with one unpaired seta.

Ventral chaetotaxy of head with  $a_1$ ,  $m_1$ , and  $p_1$ , but apparently lacking  $m_2$  (Fig. 18 e). Abd<sub>1</sub> with 1 + 1 seta beside the ventral tube. Abd<sub>2</sub> with 1 anterior seta, and 2 + 3 (2 specimens) or 3 + 3 (1 spec.) setae in posterior row. For the chaetotaxy of abd<sub>3-6</sub>, I refer to Fig. 18 d.

Discussion. Presently, only two species of *Xenyllodes* having 2 + 2 eyes are known, viz., *bayeri* Kseneman, 1935, from Central Europe, and *X. ghilarovi* Martynova, 1964, very briefly described from the USSR (Kursk). The new species differs from *bayeri* by being much more slender, the large, triangular, sunken postantennal organ, the dentes not being tuberculate, and the subempodial setae being much longer. *X. ghilarovi* is differentiated from *bayeri* rather concisely: "Postantennal organ large, triangular. Body without pigment". The only accompanying drawing shows two eyes set fairly close to each other (separated by less than half eye diameter) and the postantennal organ superficial.

The name was chosen not only because part of the material was collected in Knossós, the palace of the Minotauros, but also because I was reminded of this legendary being by the shape of the mucro, which has some resemblance to the emblem of the holy bull.

#### ***Brachystomella parvula* (Schäffer, 1896)**

Material: sample 16: 2 ♀ and 1 ♂; 17: 1 juv.; 27: 7 ♀, 4 ♂, and 2 juv.; 36: 4 ♀; 41: 4 ♀ and 1 juv.; 42: 1 ♀; 43: 1 juv.; 45: 3 juv.

This material will be dealt with by Dr. Z. Massoud and Dr. J. Najt, who are preparing a revision of this species.

#### ***Friesea afurcata* Denis, 1926**

Introductory remarks. The Cretan material contained a fine series of this species. It was, however, by no means homogeneous material and at a first glance seemed to comprise three species, but since the differences were not considered sufficiently important, I preferred to treat the variants as three types of the same species. They are possibly to be explained by differences in post-adult development; I found no indications for an explanation in terms of ecomorphosis.

It is interesting to compare this variability with the results of Grow & Christiansen (1974), which unfortunately did not become available to me until after the completion of the present study.

#### ***Friesea afurcata* Denis, 1926, type I (Fig. 19 e-g, 20)**

Material: sample 41: 11 ♀ and 3 ♂; 49: 1 ♀; 1 ♀ from sample 41 was partially, and 2 ♀ and 2 ♂ were wholly depigmented by treatment with HCl—KClO<sub>3</sub>. One of the depigmented ♀ was squashed for a study of the mouth parts.

Description. Mean total length of 10 ♀ from sample 41 is 1.63 mm ( $s=0.14$  mm,  $s_x=0.04$  mm); mean length of 3 ♂ is 1.31 mm ( $s=0.28$  mm,  $s_x=0.16$  mm). Difference in size between the sexes significant ( $t=2.853$ ,  $df=11$ ,  $0.02>P>0.01$ ). The single ♀ from sample 39 measures 1.2 mm. Irregular bluish-grey pigmentation dis-

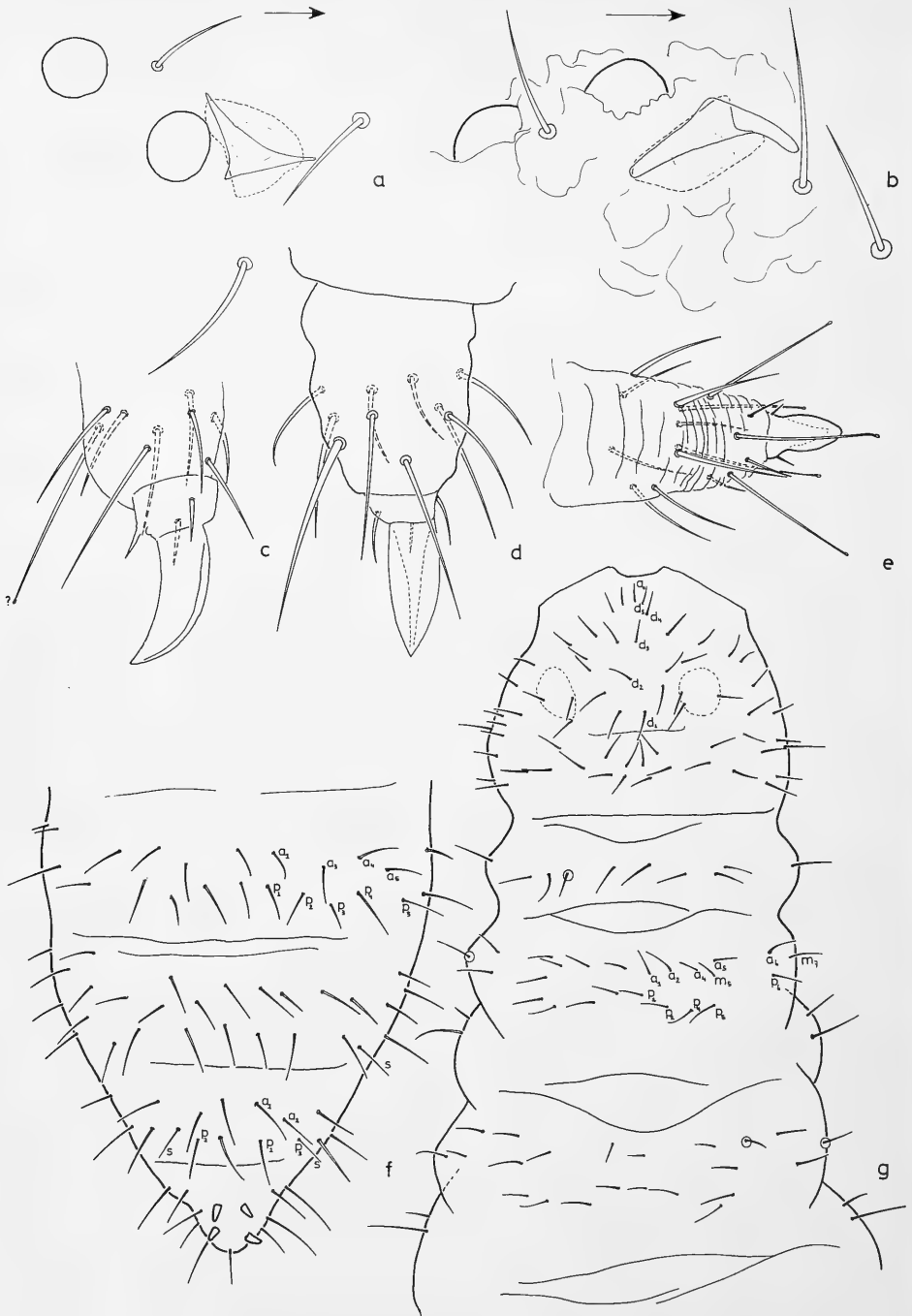


Fig. 19. *Xenyllodes minitaurus* n. sp. a, eyes and postantennal organ in perpendicular view; b, the same, oblique view; c, claw of P<sub>1</sub>; d, tibiotarsus of P<sub>1</sub>; *Friesea afurcata* Denis type I. e, tibiotarsus of P<sub>2</sub>; f, dorsal chaetotaxy of abd<sub>3-6</sub>; g, dorsal chaetotaxy of head and thorax. (Encircled hair bases refer to setae missing in the specimen from which the drawing was made.)

persed all over the body, less densely in ventral region. Eye patches dark. Integumentary granulation rather fine and regular, in abd<sub>6</sub> a bit coarser.

Ant<sub>4</sub> with retractile apical papilla, distinct strongly curved swollen sense hairs, and a number of setiform sense hairs. Ventro-distally there is a group of about eight short blunt sense hairs. Suture between ant<sub>3</sub> and ant<sub>4</sub> only visible ventrally (Fig. 20 a). Ant<sub>3</sub> with antennal organ normal; two small, parallel, rectangularly curved sense clubs in a shallow groove, guarded by two thickened sense hairs ca. 7—8  $\mu$  long (Fig. 20 c). Eyes 8 + 8. Maxilla typical (Fig. 20 f); mandible with 3 strong basal teeth, 3 smaller distal teeth with a small fourth one, and a tooth associated with the corpus of the mandible (Fig. 20 g).

Unguis with a tooth in the middle of the internal lamella, which is, however, sometimes indistinct or missing; lateral carinae without teeth. Unguiculus absent. Two inner and two outer tenent hairs with a barely perceptible distal dilatation (Fig. 19 e).

Ventral tube with 4 + 4 setae; retinaculum and furca completely absent. Male genital papilla with about 25 setae, female genital orifice with about 15 associated hairs. Anal spines 4, strong, almost straight, arranged in a square, totally differentiated from normal hairs (Fig. 20 b).

Dorsal chaetotaxy (Fig. 19 f, g) composed of coarse, long, distinctly rugose setae (ventral chaetotaxy composed of smooth smaller hairs). Cephalic chaetotaxy with setae p<sub>1-4</sub>, c<sub>1-4</sub>, a<sub>0</sub>, d<sub>1-5</sub> (d<sub>2</sub> is unpaired), sd<sub>1-5</sub>, oc<sub>1-3</sub>. No setae v. Th<sub>1</sub> with 4 + 4 setae. Th<sub>2</sub> with a<sub>1-2</sub>, a<sub>4-6</sub>, m<sub>5</sub>, m<sub>7</sub>, p<sub>1-2</sub>, p<sub>4-6</sub>; p<sub>4</sub> = ss. Th<sub>3</sub> differs from th<sub>2</sub> only but constantly by lacking a<sub>2</sub>. Subcoxae with 1, 2, 2 setae. Abd<sub>1-3</sub> with a<sub>1</sub>, a<sub>3-5</sub>, p<sub>1-5</sub>; p<sub>5</sub> = ss. Chaetotaxy of abd<sub>4</sub> is rather irregular, especially in the a row. It seems as though normally a<sub>1-5</sub> are present. In the posterior row the normal situation is: p<sub>1-2</sub>, p<sub>4-5</sub>; p<sub>5</sub> = ss. In abd<sub>5</sub> a<sub>1-3</sub> are present, as well as p<sub>1-3</sub>. Very often not p<sub>3</sub> (the normal case) but p<sub>2</sub> = ss; in the present material this only happens asymmetrically, but this might explain the situation illustrated by Da Gama (1964) for *F. afurcata*, where p<sub>2</sub> is ss at both sides of abd<sub>5</sub>.

Ventral chaetotaxy of head with only a<sub>1</sub> and m<sub>1</sub> (Fig. 20 e); thoracic sternites and abd<sub>1</sub> not chaetose. Abdominal sternites 2-4 with a large number of setae which are difficult to homologize (Fig. 20 d).

Diagnosis. On the basis of the keys of Gisin (1960) and Massoud (1967) one would identify the present species as *F. afurcata* Denis, 1926. This species was described from Italy, and was later reported from Germany and Austria. The species was recorded from the Lebanon by Cassagnau & Delamare Deboutteville (1955). The types have been studied in as much detail as was still possible by Da Gama (1964) in connection with a redescription of *F. ladeiroi* Da Gama, 1959. Quite recently, Dallai (1973), in connection with the description of the related *F. lagrecai*, provided additional details after topotypical material of *afurcata*. From all this it can be inferred that the Cretan material is, to say the least, very close to *afurcata*; possibly important differences are in the tenent hairs — in the Greek specimens much less distinctly clavate than as drawn by Dallai — and in the chaetotaxy of abd<sub>4</sub>. Although some ambiguity exists, partly due to different interpretations of the chaetotaxy, Cretan *afurcata* seem to have one more seta in the p row.

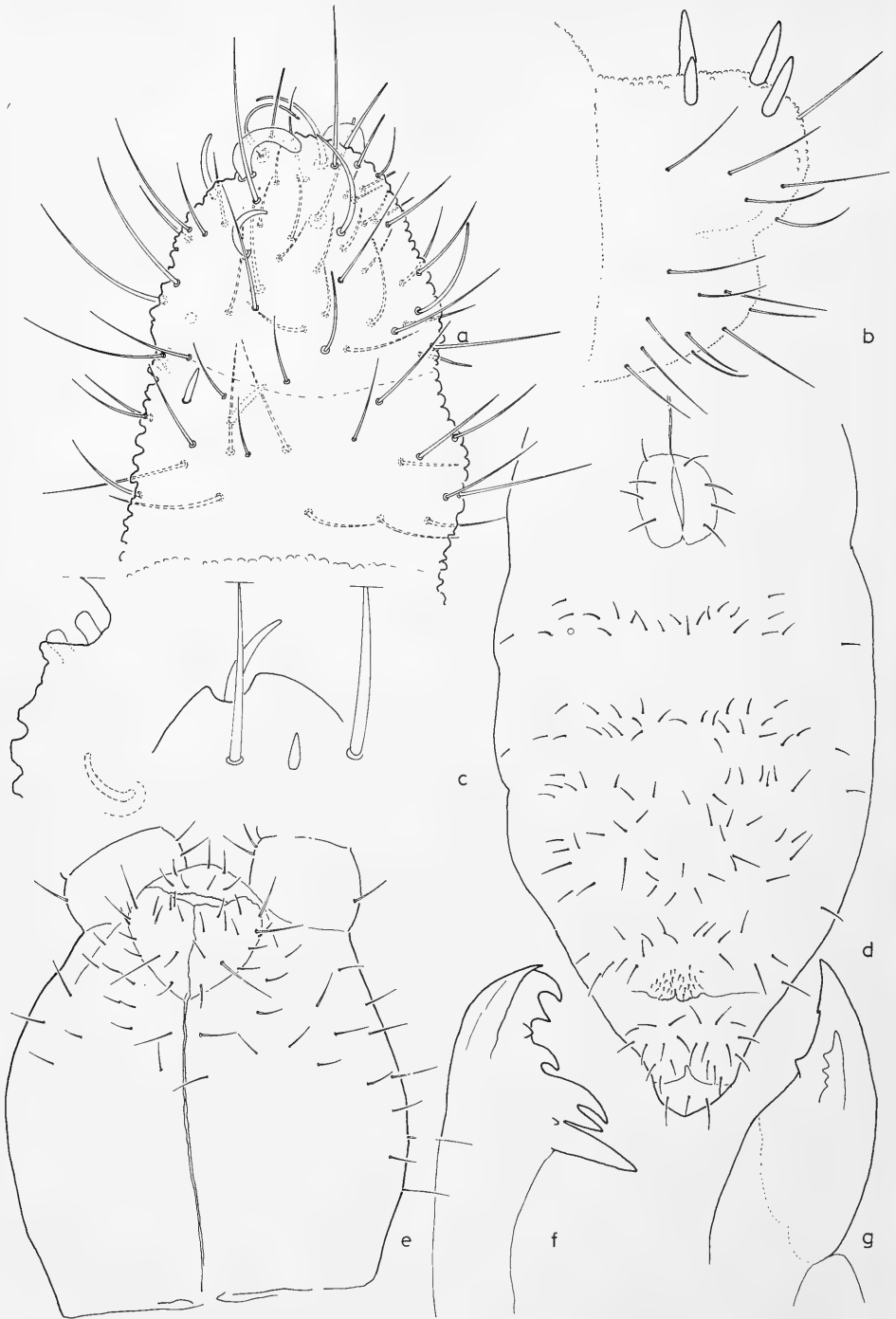


Fig. 20. *Friesea afurcata* Denis, type I. a, ant<sub>3-4</sub>; b, lateral aspect of abd<sub>6</sub>; c, antennal organ III; d, ventral chaetotaxy of abd<sub>1-6</sub>; e, ventral chaetotaxy of head; f, mandible; g, maxilla



Another species which seems very close to the present material is *Colonavis grandis* Salmon, 1949 (= *Friesea salmoni* Massoud, 1967, nom. nov. pro *F. grandis* (Salmon, 1949) nec Mills, 1934) from Campbell Island.

***Friesea afurcata* Denis, 1926, type II (Fig. 21, 22 a)**

Material: sample 16: 1 ♀; 26: 1 ♀ and 2 ♂; 36: 15 ♀, 10 ♂, and 1 specimen of unknown sex - squashed; 43: 1 ♀.

Discussion. This material differs from what I have provisionally called „type I” in the following characters:

(a) in the chaetotaxy of  $th_2$  and  $th_3$  the m row has no setae — normally! In at least one specimen  $th_3$  has a distinct  $m_s$ , in a symmetrical position (Fig. 21 d);

(b) in  $abd_3$ ,  $p_2 = ss$  (Fig. 21 a);

(c) the anal spines are much more slender or, in other words, less differentiated from normal setae;

(d) the abdominal setae are more slender, shorter, and much less rugose; often it is hard to find any rugosity;

(e) the integument of  $abd_6$  is distinctly more coarsely granulated than that of the rest of the body; this is very striking, and visible at rather low magnifications;

(f) the ventral chaetotaxy of  $abd_1$  and  $abd_2$  is much less dense (Fig. 22 a);

(g) lateral sensillae of ant. organ III longer compared to body of  $ant_4$  and to length of guarding setae (Fig. 21 b);

(h) the specimens are much smaller; the mean total length of the females from sample 36 is 0.71 mm ( $s = 0.05$  mm,  $s_{\bar{x}} = 0.02$  mm), of the males 0.62 mm ( $s = 0.06$  mm,  $s_{\bar{x}} = 0.02$  mm); the difference in size between the sexes is significant ( $t = 3.481$ ,  $df = 23$ ,  $0.01 < P < 0.001$ ); the specimens from the smaller samples lie in the same range.

The last character could be interpreted as an indication of immaturity of the material, but most of the males show active internal genitalia and testicular tissue. However, the otherwise close similarity to *afurcata* (number of anal spines, total reduction of retinaculum and furca, number of eyes, etc.) is such that I prefer provisionally to put more emphasis on the relationship between the forms around *afurcata* rather than to separate them by creating different species. Moreover, some of the characters may be related to allometric growth (structure of setae, anal spines, chaetotaxy of abdominal sternites 1 and 2), and I cannot exclude the possibility that material of type I is somewhat older than that of type II. It may be significant that Gisin (1960) mentioned for *afurcata* the unusual wide length interval of 0.8-1.6 mm.

***Friesea afurcata* Denis, 1926, type III (Fig. 22 b, c)**

Material: sample 2: 1 ♂; 40: 4 ♀ and 4 ♂.

Discussion. This material comes closest to “type II”. The mean size for the ♀ is 0.7 mm, for the ♂ 0.6 mm. This sex difference is not significant. The sensillae lateral to antennal organ III are long, even somewhat undulate. The tibiotarsal tenent hairs are even more weakly differentiated. The integument of  $abd_6$  is

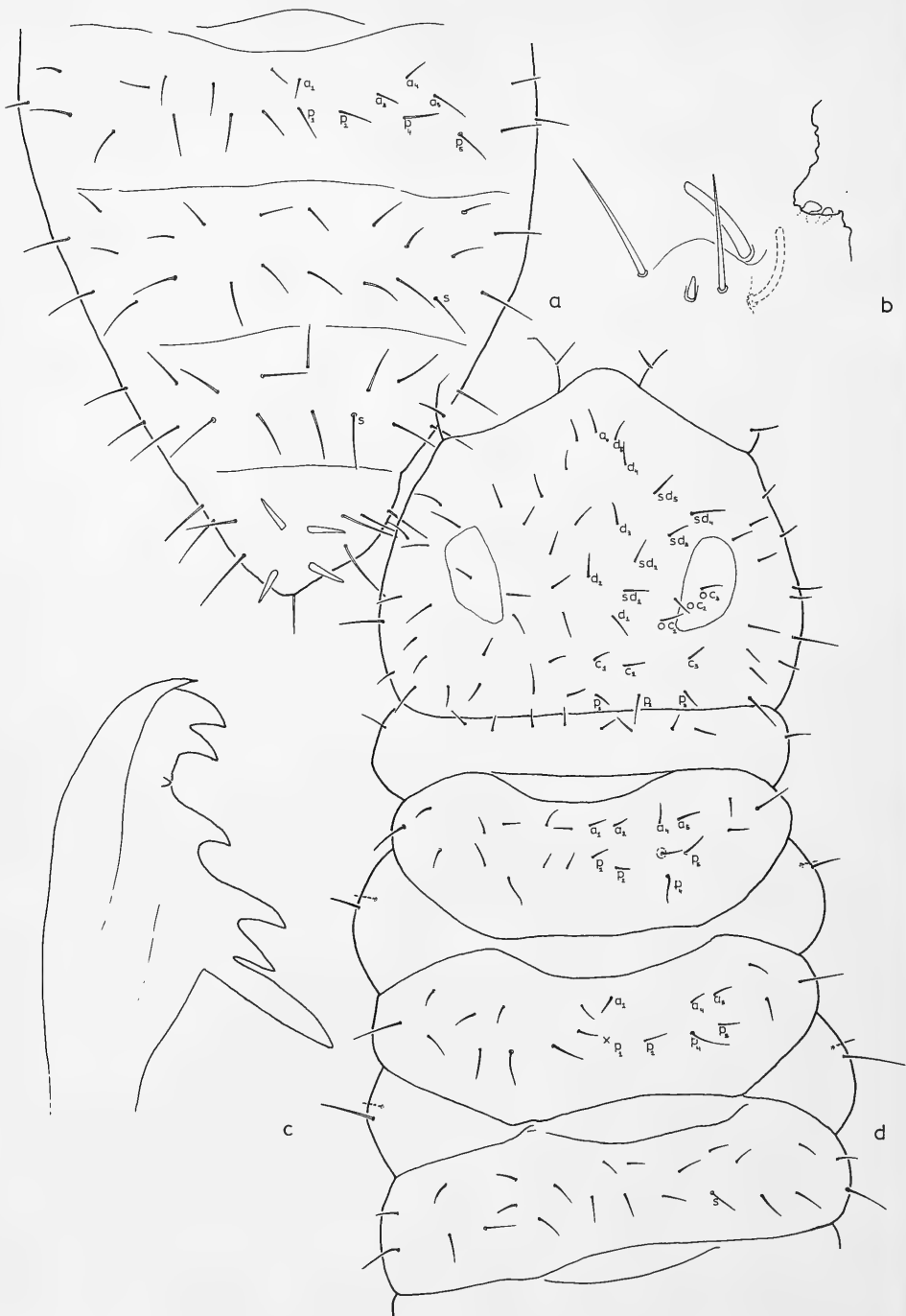


Fig. 21. *Friesea afurcata* Denis, type II. a, dorsal chaetotaxy of abd<sub>3-6</sub>; b, antennal organ III; c, mandible; d, dorsal chaetotaxy of head, thorax, and abd.; an x indicates a hair missing in the actual specimen, an encircled seta is lacking in the remainder of the specimens

differentiated in the same way, i.e., coarsely granulated. However, I am forced to place it in a type of its own — if not a species — since the setae  $a_2$  on  $abd_6$  are spiniform, and just as strongly as  $a_1$  or  $p_1$ . This brings the present material close to *F. ladeiroi* Da Gama, 1959, described from Madeira, and differentiated from *F. afurcata* by having six anal spines (shaped just like those of my *afurcata* III), the setae almost completely smooth, and only one tenent hair which is not clavate. In

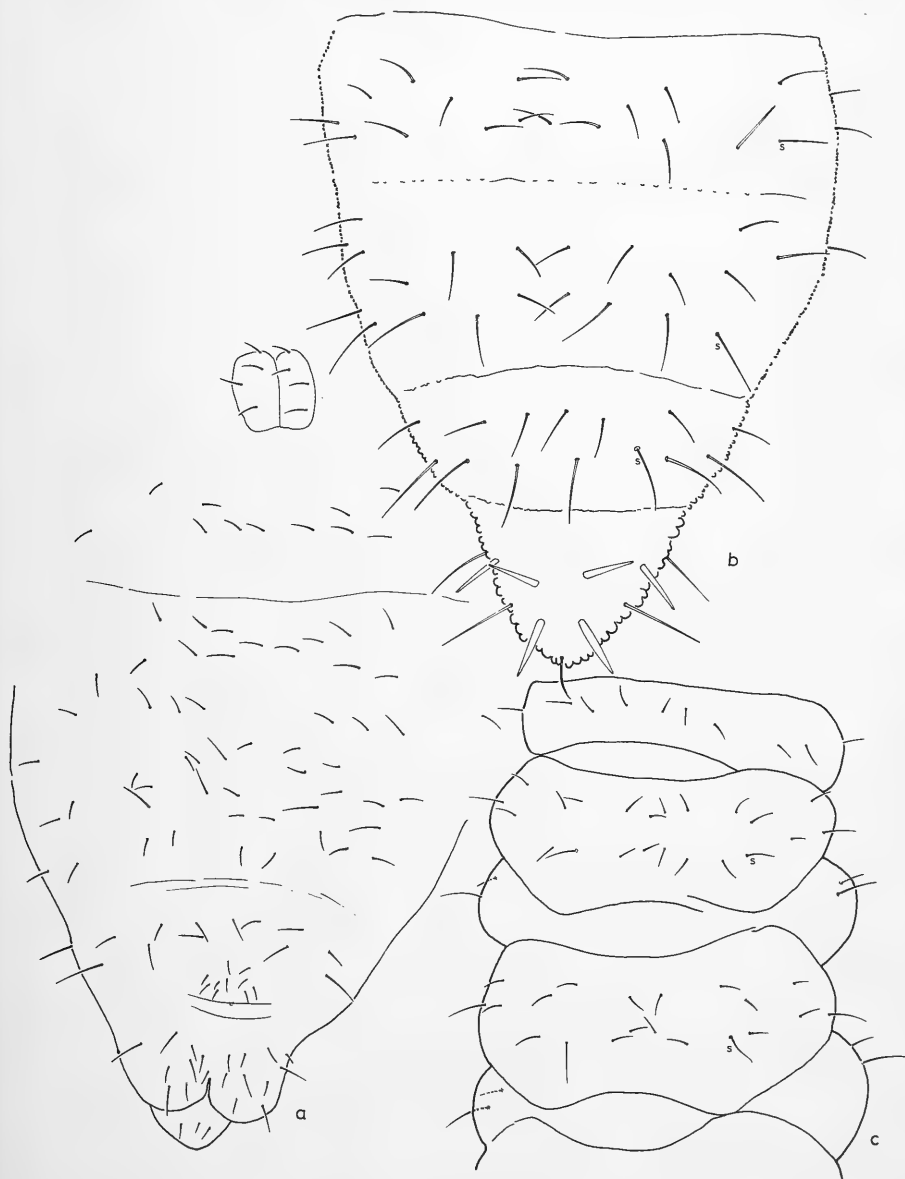


Fig. 22. *Friesea afurcata* Denis, type II. a, ventral chaetotaxy of abdomen. *Friesea afurcata* Denis, type III. b, dorsal chaetotaxy of  $abd_{3-6}$ ; c, dorsal chaetotaxy of thorax

1964, Da Gama added to these characters: absence of setae  $a_2$  in  $abd_5$  and perhaps the absence of  $a_5$  in  $th_{2-3}$ . *F. afurcata* III remains distinct from *ladeiroi* in possessing  $a_2$  on  $abd_5$ , and moreover in having  $a_5$ , but missing  $m_5$ , in  $th_{2-3}$  (I admit that if inserted a bit more caudad, the seta which is present might just as well be called  $m_5$ ; but  $a_5$  and  $m_5$  are not present at the same time anyway).

### **Friezea decipiens** Steiner, 1958 (Fig. 23 a, b)

Material: sample 25: 5 ♀ and 3 ♂.

Discussion. This species, described from Spain has recently been found by Dallai (1969 b, 1973) and Rusek (1973 b) in Italy. The species seems to have a Mediterranean distribution. Supplementary to the description by Steiner and the drawings by Rusek, I give some descriptive notes.

Mean length of the females 0.7 mm ( $s = 0.07$  mm,  $s_{\bar{x}} = 0.03$  mm); mean length of the males 0.6 mm ( $s = 0.02$  mm,  $s_{\bar{x}} = 0.01$  mm). Cephalic chaetotaxy as illustrated for *F. afurcata*. Thoracic chaetotaxy differs by the absence on  $th_{2-3}$  of  $m_5$ ; at the same time,  $a_5$  is displaced somewhat caudad, being inserted almost at the place of  $m_5$ .  $Abd_{1-3}$  with  $a_1$ ,  $a_{3-5}$ ,  $p_{1-2}$ ,  $p_{4-5}$ ;  $p_4 = ss$ .  $Abd_4$  with 3+3 setae in the a row before the 4+4 in the p row.  $Abd_5$  lacks  $a_2$  and  $p_2$  is  $ss$ . Seta  $p_1$  rather long and stiff; seta  $a_1$  and  $a_3$  distinctly longer than drawn by Rusek. The median anal spine is usually smaller than the lateral ones, and mostly but not always, almost straight (Fig. 23 b). Ventral chaetotaxy of head with  $a_1$  and  $m_1$ ; thorax and  $abd_1$  ventrally achaetose. Ventral chaetotaxy of  $abd_{3-4}$  rather imperfectly symmetrical (Fig. 23 a). All body setae very fine and smooth, except  $p_1$  on  $abd_5$  which is a bit coarser though still smooth. Subcoxae 1, 2, 2.

The material is in good agreement with the description by Steiner except that the unguis is provided with a distinct inner tooth.

### **Tremoisea cf. ossica** Cassagnau, 1973 (Fig. 23 c-e)

Material: sample 45: 1 ♂.

Discussion. It was a pleasant surprise to find a representative of the genus *Tremoisea*, described in 1973 by Cassagnau for a species from Kérkira and another from the Greek mainland, not far from Lárissa. The single specimen, measuring 1.5 mm, had its intestine filled with some dark-blue (clay?) material, showing up an unexpected array of what seem to me to be intestinal diverticula (Fig. 23 e). However interesting these may be, they impeded closer study of the specimen. But all essential traits necessary for the generic allocation are distinct: the strange mouth cone (Fig. 23 d), the multidentate mandible and the elongate Friezeinae-type maxilla, the complete eye patch, albeit lacking the postantennal organ, the abundant chaetotaxy, and so on. However, it seems to me that the chaetotaxy of my single specimen, as far as this could be studied, was not perfectly symmetrical. From the structure of the unguis (Fig. 23 c) it is evident that in any case the specimen comes close to *T. ossica*, described from Thessalia.

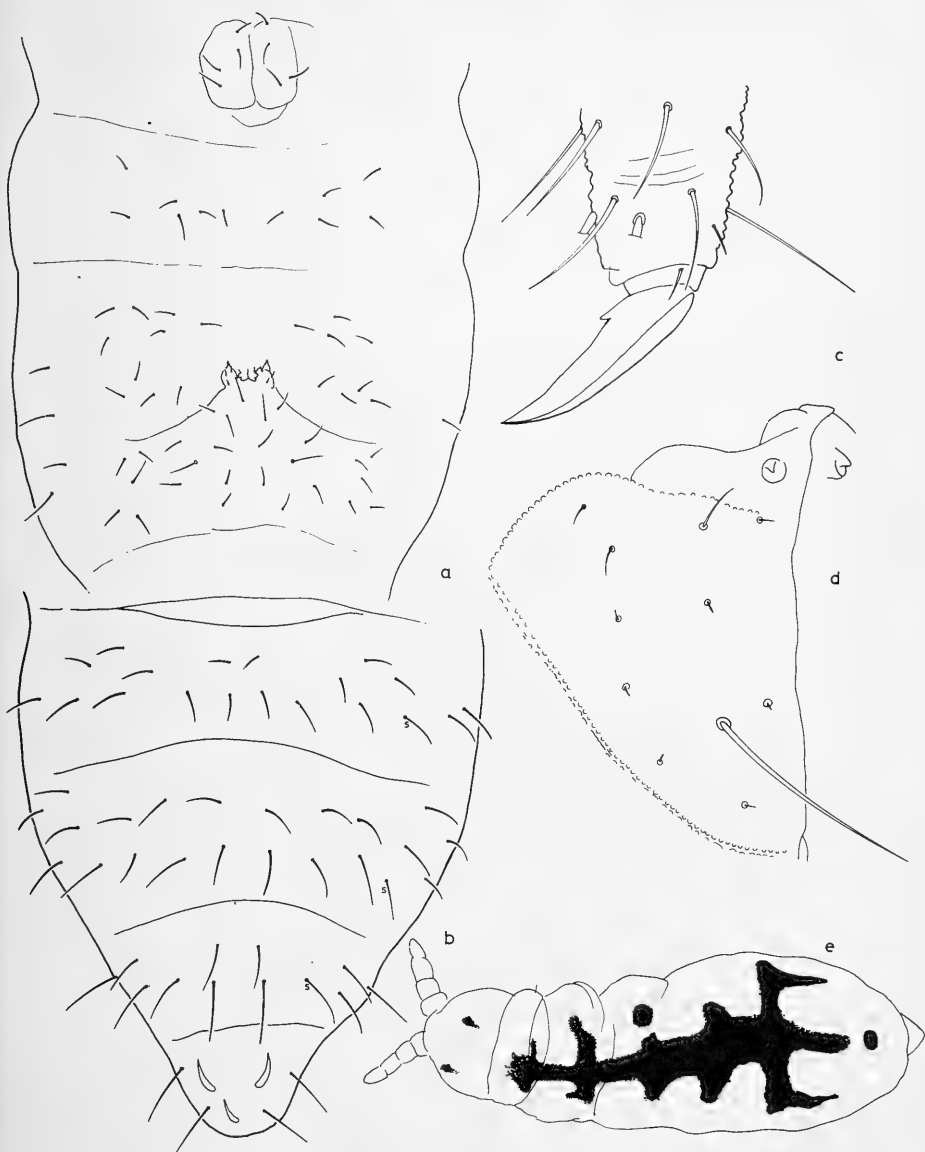


Fig. 23. *Friesea decipiens* Steiner. a, ventral chaetotaxy of  $abd_{1-4}$ ; b, dorsal chaetotaxy of  $abd_{3-6}$ . *Tremoisea* cf. *ossica* Cassagnau. c, claw of  $P_1$ ; d, mouth cone; e, habitus of cleared specimen (to show intestinal diverticula)

***Pseudachorutella* cf. *asigillata* (Börner, 1901) (Fig. 24)**

**Material:** sample 21: 1 juv., depigmented by HCl-KClO<sub>3</sub> treatment; 35: 1 juv., squashed for observation of mouth parts.

**Description.** Length 0.6 mm; irregular not very strong greyish-blue pigment on dorsum and extremities. Habitus normal. Skin granulation moderate. Antenna<sub>4</sub>

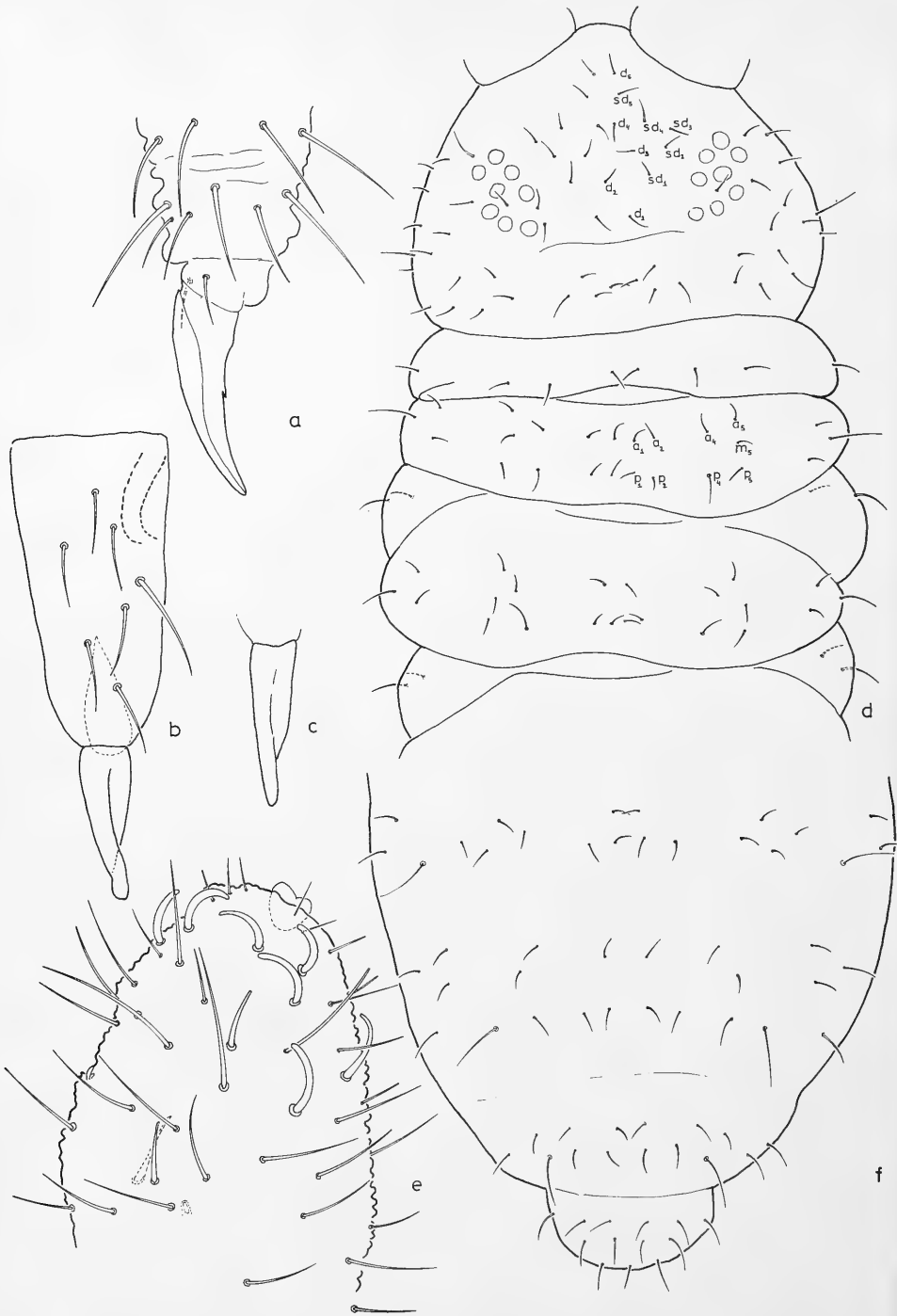


Fig. 24. *Pseudachorutella* cf. *asigillata* (Börner). a, claw of  $P_1$ ; b, posterior face of mucrodens; c, mucro; d, dorsal chaetotaxy of head and thorax; e,  $ant_{3-4}$ ; f, dorsal chaetotaxy of  $abd_{3-6}$

with apical retractile papilla superficially trilobed, and with 8 rather slender, strongly curved sense hairs; no sensory rasp. Ant<sub>3</sub> with 2 small sensillae (I could not make out whether they are straight or curved) guarded by two comparatively slender sense hairs; a small sensilla in a groove ventrally in ant<sub>3</sub> (Fig. 24 e). Eyes 8 + 8 in a well pigmented eye spot. Postantennal organ absent. Mouth cone long; mandible in one specimen three-toothed; maxilla with two lamellae, one with a small distal hook, at least the last third free. No differentiated tenent hairs. Unguiculus absent, unguis rather slender, with a small inner tooth, but without lateral teeth (Fig. 24 a).

Ventral tube with 4+4 setae. Retinaculum tridentate. Dens with 7+7 setae, mucro elongate, straight, with a narrow inner lamella gradually narrowing towards apex (Fig. 24 b, c). No anal spines.

Chaetotaxy composed of short, smooth, nowhere clavate setae; setae sensuales well differentiated. Cephalic chaetotaxy with p and c row difficult to separate, d<sub>1-5</sub> (d<sub>2</sub> unpaired), sd<sub>1-5</sub>; a<sub>0</sub> absent; oc<sub>1-3</sub> (Fig. 24 d). Th<sub>1</sub> with 3 + 3 setae. Th<sub>2</sub> with a<sub>1-2</sub>, a<sub>4-5</sub>, m<sub>5</sub>, p<sub>1-2</sub>, p<sub>4-5</sub>; p<sub>4</sub> = ss. Th<sub>3</sub> similar but lacking a<sub>2</sub>. Abd<sub>1-3</sub> with a<sub>1</sub>, a<sub>3-4</sub>, p<sub>1-5</sub>; p<sub>5</sub> = ss.

Abd<sub>4</sub> with a<sub>1</sub>, a<sub>4</sub>, m<sub>4</sub>, p<sub>1-2</sub>, p<sub>4-5</sub>; p<sub>5</sub> = ss. Abd<sub>5</sub> with a<sub>1-3</sub>; p<sub>1-3</sub>; p<sub>3</sub> = ss (Fig. 24 f).

Discussion. This material, which is very similar to that which I recorded earlier (Ellis, 1974) from Rhodes, and also shares the inconvenience of being very young, is a bit difficult to interpret. It differs in one chaetotactic detail from *asigillata* as drawn by Da Gama (1964) viz., in the presence of a seta p<sub>2</sub> in abd<sub>5</sub>. Moreover, the shape of the straight mucro, with its narrow, apically unnotched lamella, has little resemblance to that of *asigillata*. Finally, the observation of a three-toothed mandible is suggestive — but nothing is known about possible variability in this structure. I am awaiting adult material before making a decision.

### ***Pseudachorutes dubius* Krausbauer, 1898**

Material: sample 27: 1 juv.; 35: 1 ♂.

The species has already been recorded from Greece (Evvia, Cassagnau, 1971; Rhodes, Ellis, 1974).

### ***Pseudachorutes libanensis* (Cassagnau & Delamare Deboutteville, 1955) n. comb. (Fig. 25, 26 a-c)**

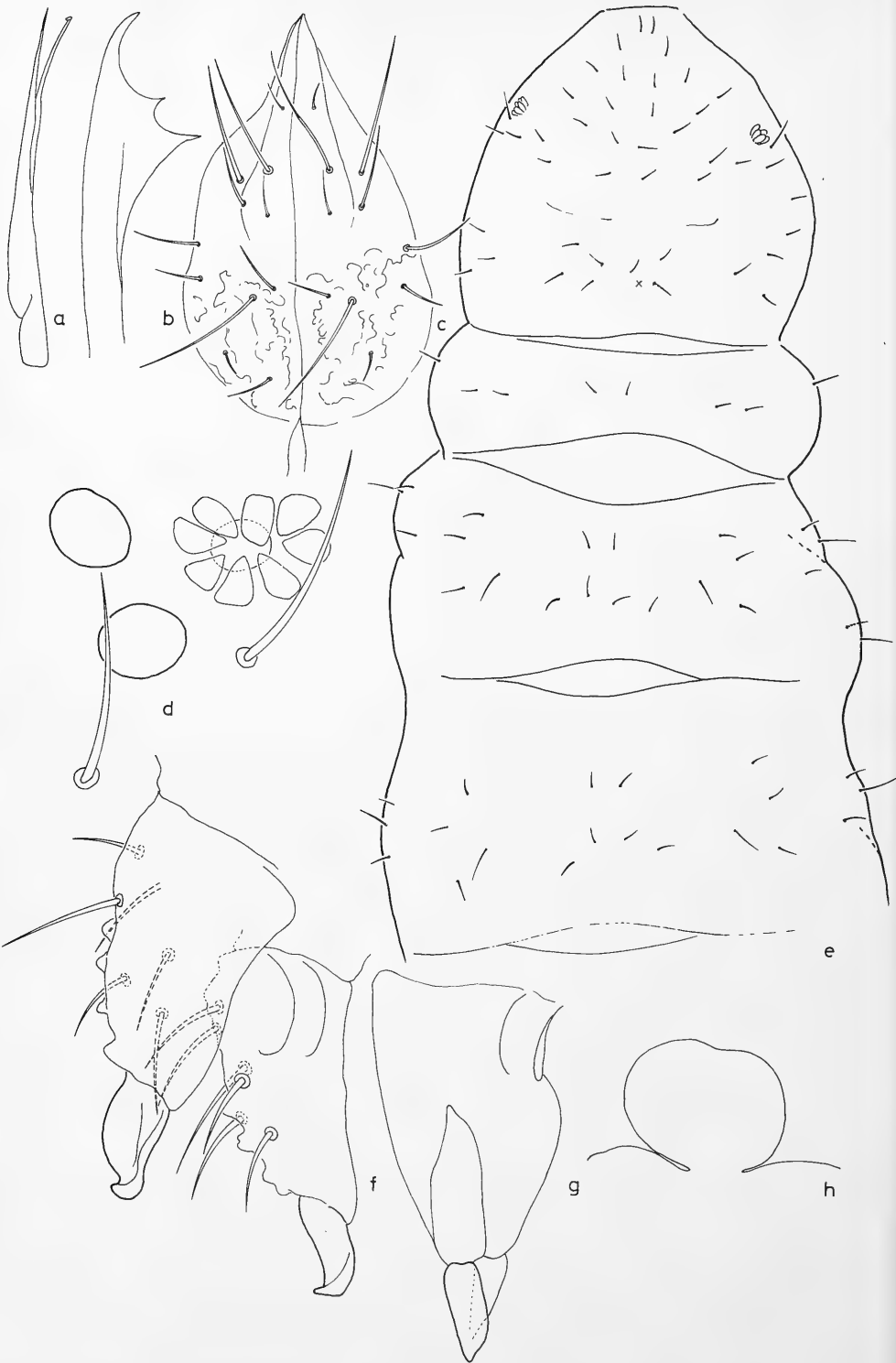
*Aethiopella libanensis* Cassagnau & Delamare Deboutteville, 1955.

Material: sample 17: 1 juv.; 32: 4 ♀ and 3 ♂; 48: 2 ♀.

Description. Mean length of the six females 0.8 mm (s = 0.16 mm, s<sub>x</sub> = 0.07 mm), that of the 3 males 0.7 mm (s = 0.10 mm, s<sub>x</sub> = 0.06 mm).

Skin granulation normal for the genus, greyish-blue pigment, not particularly dark, scattered over dorsal parts of body.

Ant<sub>4</sub> with apical bulb "apple-like": almost globular, but with a slight apical invagination (Fig. 25 h). Outer side of this antennomere with 2, inner side with 6 moderately thick curved sense hairs. Antennal organ III consists of two small,





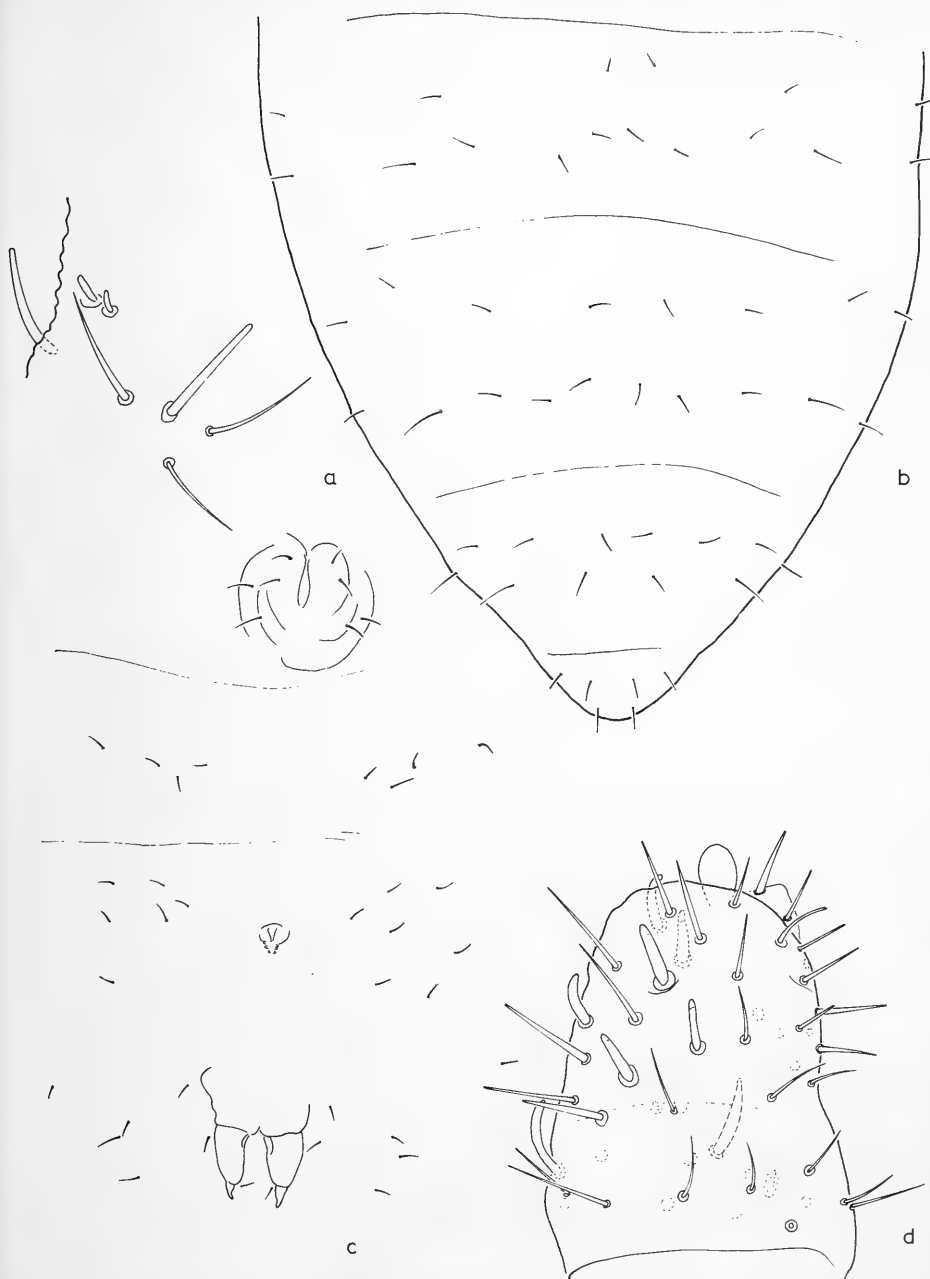


Fig. 26. *Pseudachorutes libanensis* (Cassagnau & Delamare). a, antennal organ III; b, dorsal chaetotaxy of abd<sub>3-6</sub>; c, ventral chaetotaxy of abd<sub>1-4</sub>. *Pseudachorutes* (*Pratanurida*) *mucronata* n. sp. d, ant<sub>3-4</sub>

Fig. 25. *Pseudachorutes libanensis* (Cassagnau & Delamare). a, maxilla; b, mandible; c, mouth cone; d, postantennal organ; e, dorsal chaetotaxy of head and thorax; f, furca; g, anterior face of mucrodens; h, apical papilla of antenna

straight (or almost so) sensillae, guarded by two long, slightly wavy sense hairs (Fig. 26 a). Ocelli 8 + 8. Postantennal organ with about 8 elements (Fig. 25 d). Mouth cone as long as typical for the genus (Fig. 25 c). Mouth parts studied only in transparency, normal for the genus with a needle-shaped maxilla (Fig. 25 a) and a two-toothed mandible (Fig. 25 b).

Tibiotarsus without differentiated tenent hairs. Unguis without teeth, or (seen once) with a very feeble tooth on inner lamella. Unguiculus absent.

Ventral tube with 4 + 4 setae; retinaculum tridentate. Dens with 6 + 6 setae (Fig. 25 f, g). Mucro crooked, and with inner lamella more developed than outer one. Dens with characteristic elongate area on anterior surface where the skin reticulation is missing.

Chaetotaxy composed of very short, smooth, never capitate setae. On the head are present  $p_{1-2}$  ( $p_1$  is sometimes missing),  $c_{1-2}$ ,  $d_{1-5}$ ,  $sd_{1-5}$ ;  $a_0$  and  $v$  are missing. In d row no unpaired setae.  $Th_1$  with 3 + 3 setae.  $Th_{2-3}$  identical, with  $a_1$ ,  $a_{4-5}$ ,  $p_{1-2}$ ,  $p_{4-5}$ ;  $p_4 = ss$  (Fig. 25 e). In  $abd_{1-3}$  are present  $a_1$ ,  $a_4$ ,  $p_{1-2}$ ,  $p_3$ ,  $p_5$ . In  $abd_4$  we have  $a_1$ ,  $a_3$ ,  $a_5$ , and  $p_{1-2}$ ,  $p_{4-5}$ .  $Abd_5$  with  $a_{1-3}$  and  $p_1$ ,  $p_3$ ;  $p_3 = ss$  (Fig. 26 b). No anal spines.

Discussion. The present material agrees closely with the description of *Aethiopella libanensis*, based on a single specimen from Beirut, except of course in the structure of the postantennal organ, which is said to be moruliform in the type specimen. However, even the description leaves some uncertainty as to this point, and in one of the two aspects of the postantennal organ drawn by the authors, it is almost completely pseudachorutiform. I am therefore convinced that *libanensis* was incorrectly allocated, presumably because it was described after a defective specimen.

The species comes close to *Pseudachorutes parvulus* Börner, 1901, *P. subcrassus* Tullberg, 1871, *P. crassus* Da Gama, 1964, *P. geronensis* (Massoud, 1963), and *P. pratensis* Rusek, 1973. *P. libanensis* differs from the first three species in the absence of seta  $a_2$  in  $th_2$ , and also in the combination of characters: no unpaired seta in d row on head, and  $abd_5$  carrying setae  $a_{1-3}$ ,  $p_1$ ,  $p_3$ . The main differences with respect to *geronensis* are the normal mouth cone (that of *geronensis* is very short for the genus), the straight sensillae in the ant. org. III, and the structure of the mucro. Possibly, the chaetotaxy of  $abd_5$  is also different in *geronensis*. *P. libanensis* is most closely related to *P. pratensis* Rusek, 1973. The chaetotaxy of these two species seems to be identical. Differences concern the larger number of sense hairs in  $ant_4$  (4 in *pratensis*), the shape of the sensillae in the antennal organ III (short, distally swollen clubs in *pratensis*, straight rodlets in *libanensis*), and especially the form of the mucro, which is normal for the *parvulus* group in *pratensis* but hooked in *libanensis*. Useful distinctions are perhaps offered by the slightly larger number of elements in the PAO and the distinct tooth on the unguis in *pratensis*.

### ***Pseudachorutes (Pratanurida) mucronata* n. sp. (Fig. 26 d, 27, 28 a-c)**

Material: sample 17: 1 ♀ (holotype); 36: 1 ♀.

Description. The holotype female measures only 0.4 mm; the other specimen is 0.6 mm. Both specimens have the genital orifice open, but provided with only a few setae, and it is possible that they are not completely mature. Pigmentation

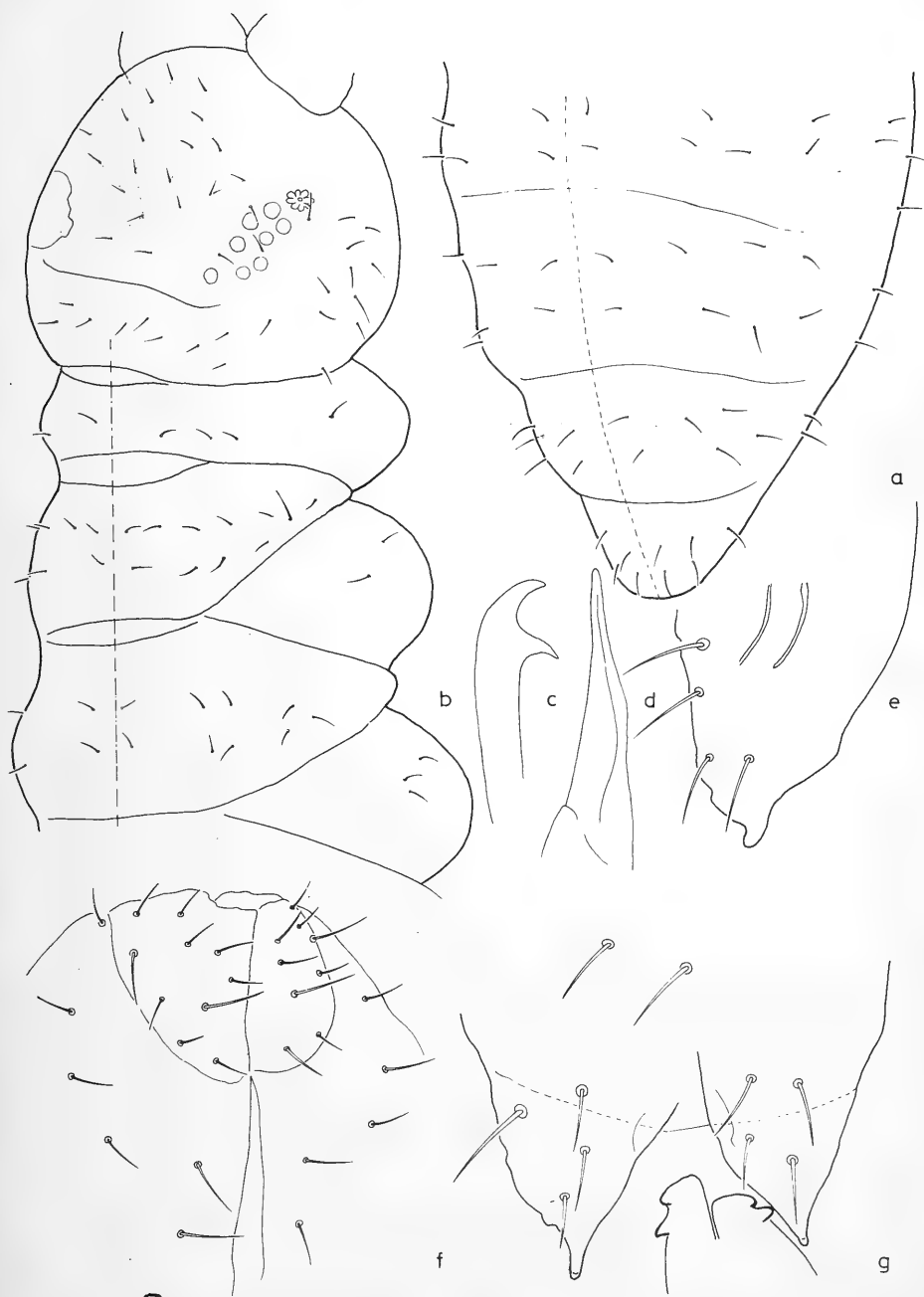


Fig. 27. *Pseudachorutes (Pratanurida) mucronata* n. sp. a, dorsal chaetotaxy of  $abd_{3-6}$ ; b, dorsal chaetotaxy of head and thorax; c, mandible; d, maxilla; e, mucrodens in lateral aspect; f, ventral chaetotaxy of mouth region; g, furca and retinaculum

greyish-blue, but particularly strong. Eye patch darker. Integument finely and regularly reticulate, as in *Pseudachorutes* s.s.; no *Neanura*-type reticulation present. Habitus as in a normal *Pseudachorutes*.

Antenna<sub>4</sub> with retractile apical papilla undivided; interior face with 4, outer face with 2 curved and thickened sense hairs; no sensory rasp (Fig. 26 d). Antennal organ III two minute, erect clubs, almost without integumental plica, guarded by two strong sense hairs; antenna<sub>3</sub> moreover with a sensilla in a groove (Fig. 28 c). Eyes 8+8. Postantennal organ with 7-8 elements arranged in a circular rosette (Fig. 28 a, b). Mouth cone short (Fig. 27 f). Mouth parts (seen in transparency): mandible with two teeth only (Fig. 27 c), maxilla needle-shaped with two lamellae (Fig. 27 d).

Unguis without inner or lateral teeth; no unguiculus, no differentiated tenent hairs.

Ventral tube with 4+4 setae; retinaculum bidentate. Furca present but reduced. Dentes rather short, almost triangular, with 4+4 setae; mucro present, reduced to no more than a hook-like continuation of the dens, not visibly separated from the latter (Fig. 27 e, g). Female genital orifice small, with 5 setae. No anal spines.

Chaetotaxy composed of short, smooth setae. It is almost impossible to homologize the setae, partly because only two specimens are available, but especially because the sensory setae are not visibly differentiated. Cephalic chaetotaxy with rows p and c incomplete; setae v and a<sub>0</sub> are lacking; d<sub>1-5</sub> (d<sub>2</sub> is unpaired, called d<sub>0</sub> in the papers of Da Gama et al.), sd<sub>1-5</sub>. Th<sub>1</sub> with 3+3 setae. Th<sub>2</sub> with 4 setae in the a row and 3 setae in p row in discal area; th<sub>3</sub> identical except one seta missing in a row. In th<sub>2-3</sub>, neither shows a distinct seta p<sub>2</sub> (Fig. 27 b). Subcoxae 1, 2, 3.

Discussion. The new species fits easily into the genus *Pratanurida*, created in 1973 by Rusek for his new *P. cassagnai* from Central Europe. That species was redescribed shortly afterward by Dunger, 1974. Briefly, *Pratanurida* is *Pseudachorutes* with the furca reduced. *Pseudachorutes mucronatus* is easily distinguished from *cassagnai* by its mucronate dens having 4+4 setae, the less coarse reticulation, the absence of seta a<sub>0</sub> on the head, the apparently real absence of setae p<sub>2</sub> in th<sub>2-3</sub>, and perhaps also in the higher number of postantennal elements: 7-8 as against 4 (Rusek) or (4) 5-6 (Dunger) in *cassagnai*.

For a discussion concerning the position of *Pratanurida* and *Stachorutes Dallai*, 1973, intermediate between *Pseudachorutes* and *Micranurida*, I refer to Rusek (1973a) and Dunger (1974). I might only add that a tendency toward reduction of the dens is not altogether absent in *Pseudachorutes*, as indicated by *P. boernerii* Schött, 1902; this is why I consider *Stachorutes* a good genus, but *Pratanurida* a subgenus.

### *Neanura granulata* Cassagnau & Delamare Deboutteville, 1955 (Fig. 28 d)

Material: sample 6: 1 ♀ and 1 ♂; 35: 1 ♀.

Description. Since the present material differs somewhat from the original description, which was based on 10 specimens from the Lebanon, I shall describe the Cretan specimens in some detail.

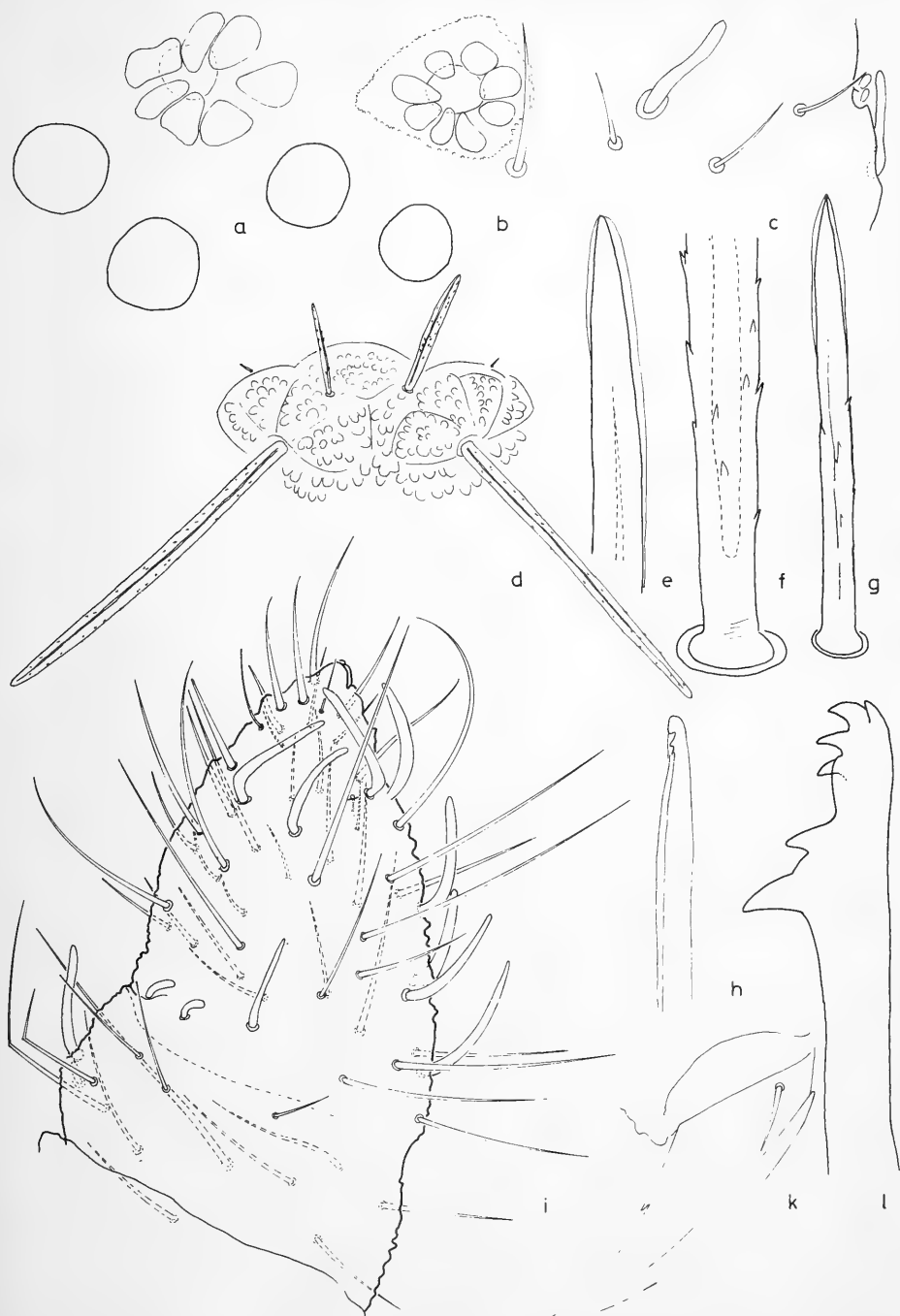


Fig. 28. *Pseudachorutes (Pratanurida) mucronata* n. sp. a, b, postantennal organs; c, antennal organ III. *Neanura granulata* Cassagnau & Delamare. d, chaetotaxy of tubercles di-di on abd. *Lathriopyga anthrenoidea* n. sp. e, f, apex and base of a long macrochaeta; g, small macrochaeta; h, maxilla; i, left antenna<sub>3-4</sub>; k, unguis P<sub>3</sub>; l, mandible

Length of male 1.1 mm; females 0.9 (sample 6) and 1.4 mm (sample 35). (This is at least 1 mm smaller than the original material, and some difference must possibly be explained by allometric growth). Colour in alcohol totally white, except the 2+2 lively blue eyes. Skin moderately granulate for the genus, more so on the tubercles, which are well differentiated by their coarser granulation and by their being elevated and provided with re-inforcement ridges. Antennae typical for the genus, apical bulb only indistinctly trilobate. Mouth parts also normal with needle-shaped maxilla and simple tridentate mandible. Claw toothless, no tenent hairs.

Ventral tube with 4+4 setae, rudiment of furca barely distinguishable, only three setae present at this location. Sixth abdominal segment completely visible from above.

Hairs of varying length, distinctly rugose with a pronounced double contour.

In the following Table 3 distinction is made between long (L) and short (S) macrochaetae, microchaetae (m), and setae sensuales (s). A macrochaeta is considered short if it is at most half as long as a seta in the same or a bordering tubercle. This denotation is only useful for the dorsal chaetotaxy; it loses its clarity for e.g. the lateral cephalic chaetotaxy. Fusion of tubercles is indicated by parentheses around the setal code. The anteromedian cephalic tubercle is not attached to the central one (LSS+LSS); central tubercle (LSS+S+LSS); ocular tubercle LLs; lateral tubercles of head LLLSmmm.

Note. In their drawing of abd, the authors of the species indicate that the fusion of the dorso-internal tubercles on that segment is rather incomplete, although they state in the text that the tubercles are fused along the median line. However, Massoud (1967), who studied the types, keys *granulata* with the species having these tubercles free, and this may raise some doubt about my identification.

The microchaetae on the dorso-internal tubercles of abd, are extremely small, sometimes even shorter than the diameter of a skin granule, and difficult to detect (Fig. 28 d). This not only differs from what the authors depicted, but may also confuse identifications when only the gross seta number is indicated.

Other points of divergence from original description are the full separation between central and anterior cephalic tubercle (perhaps not a very important

Table 3. Number of setae on dorso-internal (di), dorso-external (de), dorso-lateral (dl), and lateral (l) tubercles in *Neanura granulata*

	di	de	dl	l
head (posterior row)	LS	LS	LLSS	
thorax 1	S	SS	L	
2	LSS	LSs	LLSs	
3	LSS	LSsm	LSSs	
abdomen 1	LS	LSsm	LS	LSs
2	LS	LSsm	LS	LSs
3	LS	LSsm	LS	LSs
4	LS	LSs	LSS	LSs
5	(LSm + LSm)	(LLSSss)		
6	(LLLLSSS)			

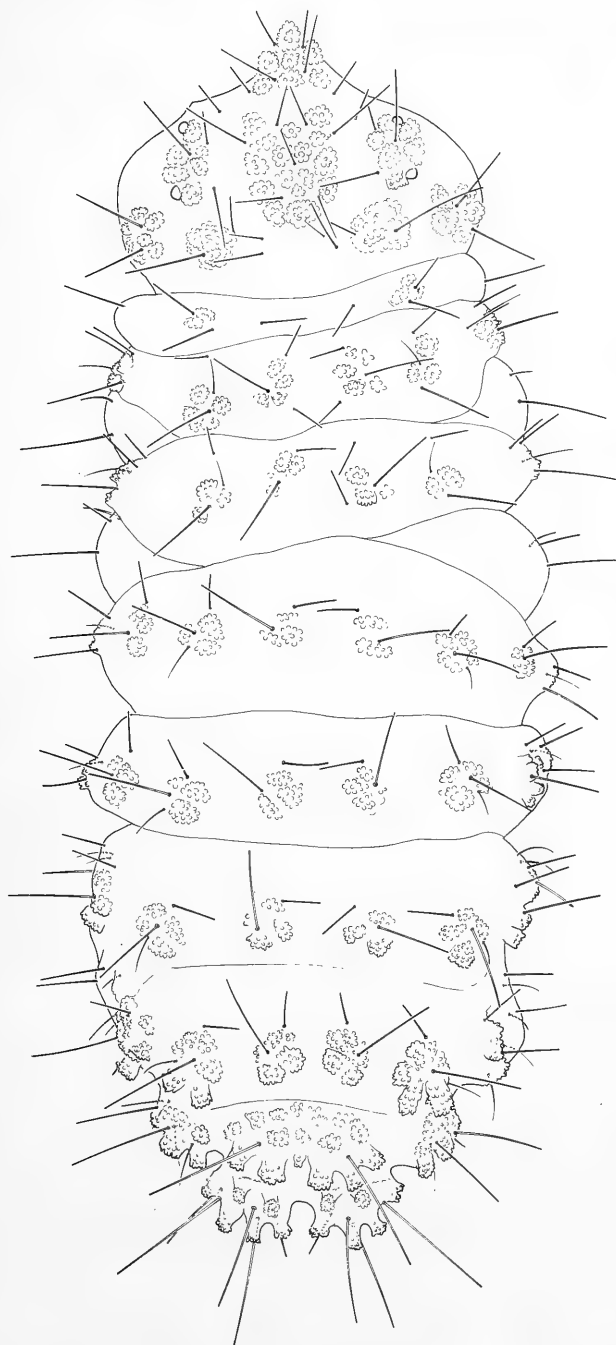


Fig. 29. *Neanura cretensis* n. sp., dorsal chaetotaxy

point, since the authors report having encountered difficulties in delimiting the tubercles) and the presence of an unpaired seta  $d_2$  in the central tubercle.

If this description is compared with that of *N. tetrophthalma* (Stach, 1929) given by Dunger (1966), it is evident that the differences between the two species are feeble indeed. The most useful criterion seems to be the relative lengths of hairs, as Dunger has already remarked, especially with respect to the central cephalic tubercle (*tetrophthalma* has seta  $sd_2$  long and stout in the central tubercle, the others are very thin and short;  $d_2$  is unpaired — as in the present material!).

***Neanura cretensis* n. sp. (Fig. 29)**

Material: sample 27: 1 ♀, holotype.

Description. Length only 0.7 mm; nevertheless, the specimen seems fully adult, the genital orifice having about 16 setae on anterior lip. Blue pigment dispersed in irregular dots all over the body; eye patches intensely black. Integument between the tubercles moderately granulated, in the tubercles rather strongly granulated, posteriorly even more so. Especially the posterior tubercles are very strong. Ocelli 2+2. Sixth abdominal segment completely visible from above.

Antenna normal, apical papilla distinctly trilobed, sense hairs distinct. Mouth cone long, mouth parts not dissected, apparently normal for the genus. Unguis toothless, unguiculus absent. Ventral tube with 4+4 setae. Furca rudiment not recognizable.

Tubercles. Central and anterior cephalic tubercles free. Dorso-internal tubercle on head hind margin without rosette, as is the dorso-internal one in th. Dorso-internal tubercles on abd, fused, dorso-external ones fused with the lateral tubercles.

Chaetotaxy (Fig. 29). Macrochaetae without double contour, almost without serrations or granulations, not constricted at base. True microchaetae, which are distinct in *granulata*, are almost lacking. Again with the denotation: L: long macrochaeta, S: short macrochaeta (relative to macrochaetae in the same or bordering tubercles), m: microchaeta, s: sensory seta, the chaetotaxy is as indicated in Table 4. Head. central tubercles (LSS + S + LSS), anterior tubercle: (LSS + LSS), ocular tubercle: LLS, lateral: LLLmmm. Between central tubercle and antennal base a free seta S.

Discussion. This is again a species closely resembling *N. tetrophthalma* (Stach, 1929). This and some related species have been treated recently by Dunger (1966). *N. cretensis* differs from *N. tetrophthalma tatricola* (Stach, 1951) by having well-pigmented body and eyes; it differs from *N. t. lusatica* Dunger, 1966, by having the macrochaetae neither granulate nor basally constricted, and also in the different length proportions of the macrochaetae (most distinct in central cephalic tubercle and abd<sub>3</sub>). *N. cretensis* differs from typical *tetrophthalma* by having the unguis toothless, and from all mentioned taxa by having the tubercles much more developed.

***Lathriopyga anthrenoidea* n. sp. (Fig. 28 e-l and 31)**

Material: sample 25: 1 juvenile, holotype, and 3 more juveniles; 43: 1 juv.

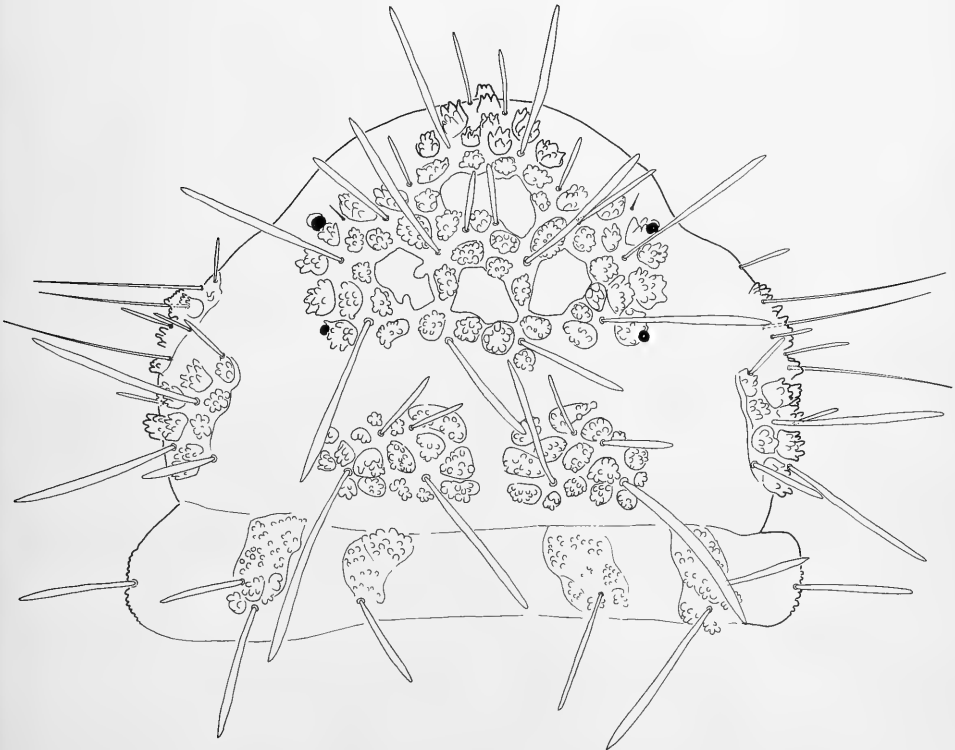
Description. Length of the largest specimen, the holotype, is 1.4 mm; others



Table 4. Number of setae on dorso-internal (di), dorso-external (de), dorso-lateral (dl), and lateral (l) tubercles in *Neanura cretensis* n. sp.

	di	de	dl	l
head (posterior row)	LS	LS	LL	
thorax 1	S	LSs	L	
2	LSS	LSs	LSSsm	
3	LSS	LSs	LSSs	
abdomen 1	LS	LSs	LS	LSs
2	LS	LSs	LS	LLs
3	LS	LSs	LS	SSss
4	LS	LSs	LLS	SSSSss
5	(L + L)		<u>LLSS</u>	
			LLSSss	
6		LLLSS		

range from 1.1.-1.3 mm (a mean is of course not meaningful in immature material). Habitus normal for the genus, due to the very long macrochaetae not unlike that of a carpet beetle larva, *Anthrenus*. Abd<sub>6</sub> completely hidden. Pigmentation wholly absent except for the 2 + 2 strongly dark-blue pigmented eyes. Skin granulation basally not very strong, well spaced. Tuberculation in the rosettes not very strong though distinct.

Fig. 30. *Lathriopyga longiseta* (Caroli), dorsal chaetotaxy of head and th<sub>1</sub>

Ant<sub>4</sub> with trilobed, not very distinct apical papilla and 8 sense hairs. Antennal organ III two sensillae, strongly bent in the same direction, guarded by a strong ventral and a weaker dorsal sense hair (Fig. 28 i). (Skin granulation of antenna rather uneven. Dorsal part of ant<sub>1</sub>, and whole basal part of ant<sub>4</sub> rather coarsely granulate, other parts, especially dorsal part of ant<sub>3</sub> weakly granulate).

Eyes 2 + 2. Mouth cone long; mouth parts not dissected; in transparency a 6-toothed mandible is visible, with basal tooth strongly developed (Fig. 28 l), and a needle-shaped maxilla with two lamellae which are closely appressed (fused or not) and provided with some apical denticulation (Fig. 28 h).

Feet plump, with a distinct tooth on inner lamella; lateral lamellae toothless (Fig. 28 k). Subcoxae with 1, 3, 3 setae. Ventral tube with 4 + 4 setae. Furca rudiment a median boss with some 8 setae.

Vestiture consisting of very heavy, blunt, distinctly rugose, apically winged macrochaetae of variable length, often conspicuously long, a few minute microchaetae, some sensory setae, and ventrally shorter, undifferentiated setae. The dorsal chaetotaxy is summarized in Table 5 (cf. also Fig. 31).

Table 5. Number of setae on dorso-internal (di), dorso-external (de), dorso-lateral (dl), and lateral (l) tubercles in *Lathriopyga anthrenoidea* n. sp.

	di	de	dl	l
head (posterior row)	LS	L	LLSSS	
thorax 1	L	LS	L	
2	LSS	LSs	LSSs	
3	LSS	LSSs	LSSs	
abdomen 1	LS	LSSs	LS	LSs
2	LS	LSSs	LS	LSs
3	LS	LSSs	LS	LSs
4	LS	LSs	LSSs	SSSs
5	LS		LLSSSS	

On the head all tubercles are free and well developed. The apical tubercle has setae (LS + SL), the central tubercle has (LSS + SSL) and lacks an unpaired seta, ocular tubercle has LLm, lateral tubercle LLLSSmm.

Discussion. The complete absence of fusion of tubercles makes this species very distinctive. This is why I venture to describe the new taxon on the basis of the present meagre material. Also, the distinct tooth on the unguis (which is, however, much less strongly developed than in *longiseta* (Caroli, 1912) and *hellenica* Ellis, 1974) is a rather divergent character. The thoracic chaetotaxy points to an affinity with the *L. phlegraea* group, but there the dorso-internal tubercles are fused in abd<sub>3</sub>.

### ***Lathriopyga longiseta* (Caroli, 1912) (Fig. 30)**

Material: sample 35: 1♂.

The single specimen, measuring 1.1 mm, agrees well with the original description and the more detailed description given by Da Gama (1964). The

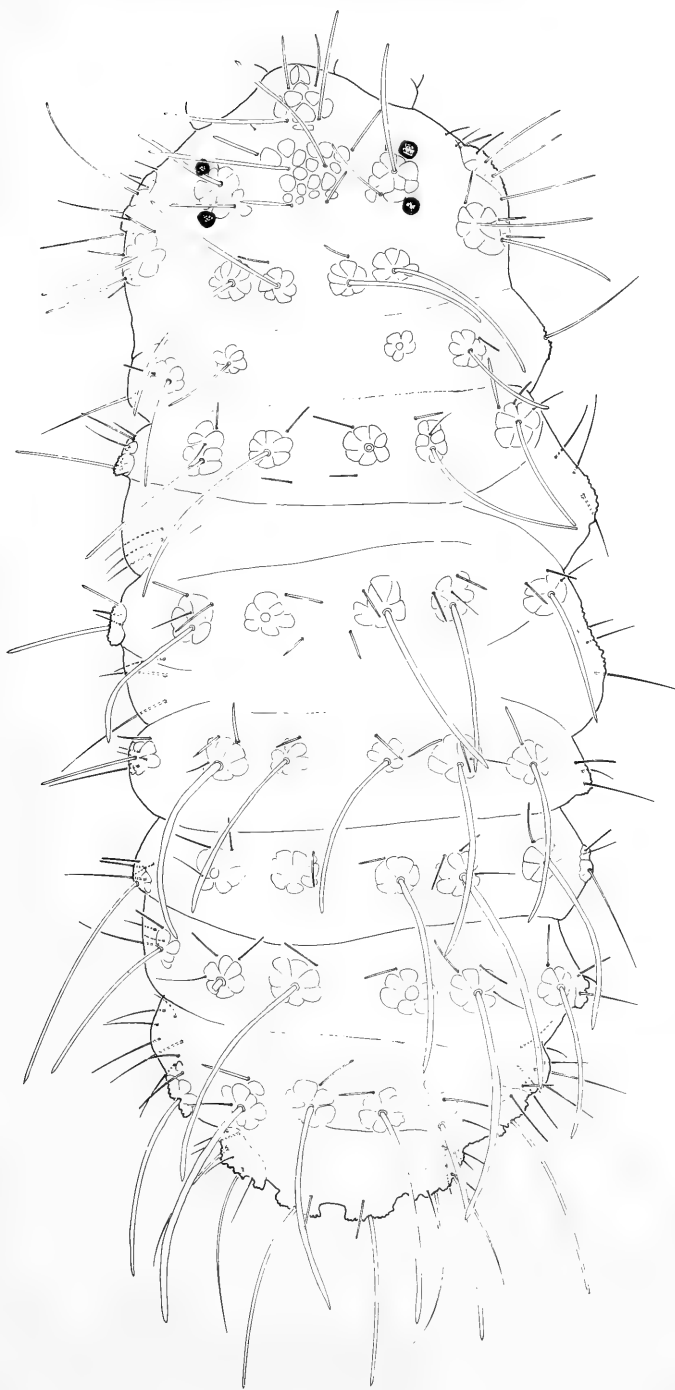


Fig. 31. *Lathriopyga anthrenoidea* n. sp., dorsal chaetotaxy

species has been recorded from Italy, Corsica, Madeira, Yugoslavia, and — since the synonymy with *L. hystrix* (Bagnall, 1940) was established by Lawrence in 1970 — England. The near relative *L. hellenica* Ellis, 1974, was described from Rhodes.

#### ISOTOMIDAE

##### ***Coloburella linnaniemii* (Denis, 1937)**

Material: sample 21: 2 juv.

Their immaturity taken into consideration, the two specimens are in good agreement with the redescription of *C. linnaniemii* given by Rusek (1972). The only notable deviation is the somewhat longer furca — the tip of the mucro reaches onto abd<sub>2</sub> over about ½ segment length. The species is now known from Italy and Crete; the near relative *C. cassagnai* Rusek, 1972, occurs in the Pyrenees.

##### ***Tetracanthella* cf. *hygropetrica* Cassagnau, 1954 (Fig. 32a)**

Material: sample 19: 9 immature specimens, only some of recognizable sex (2 ♀, 2 ♂).

Discussion. A gradual intergradation seems to exist from *T. tuberculata* Cassagnau, 1954 (described from the Sierra de Guadarrama, since then recorded from Portugal, the Pyrenees, Corsica, Italy, Yugoslavia, and the USSR), through *T. hygropetrica luxemburgensis* Stomp, 1968 (Luxemburg) and *T. h. matthesii* Da Gama, 1959 (Madeira), to *T. h. hygropetrica* (described from the Pyrenees, recorded from Portugal and Spain as well as from Italy). In fact, the best argument in favour of the validity of *luxemburgensis* and *matthesii* is their isolated occurrence.

The present material is, due to its immaturity, difficult to identify. It has a manubrium/dens ratio of about 6/5 (Fig. 32a), which comes closest to the Portuguese *hygropetrica hygropetrica* described by Da Gama (1964). In the present material reticulation is mixed and fine, mostly as narrow as the diameter of the hair rings, locally narrower. A smooth area occurs only in postero-median part of abd<sub>4</sub>.

##### ***Isotomodes trisetosus* Denis, 1923**

Material: sample 13: 1 ♀.

In her monograph of the genus, Da Gama (1963) gives records from South-Central Europe, Madeira, the Azores, and Peru.

##### ***Folsomides parvulus* Stach, 1922 (Fig. 32b, c)**

Material: sample 16: 3 ♀ and 2 juv.; 29: 4 juv.; 30: 5 ♀ and 14 juv.; 35: 1 ♀ and 5 juv.; 36: 2 ♀; 37: 1 ♀; 38: 1 ♀; 43: 13 ♀ and 13 juv.; 44: 6 ♀ and 6 juv.; 45: 1 ♀.

Discussion. My description and notes on variability in material from Rhodes (Ellis, 1974) are also applicable to the present material. The eye number is invariably 2 + 2; the eyes are sometimes devoid of pigment, especially in juveniles

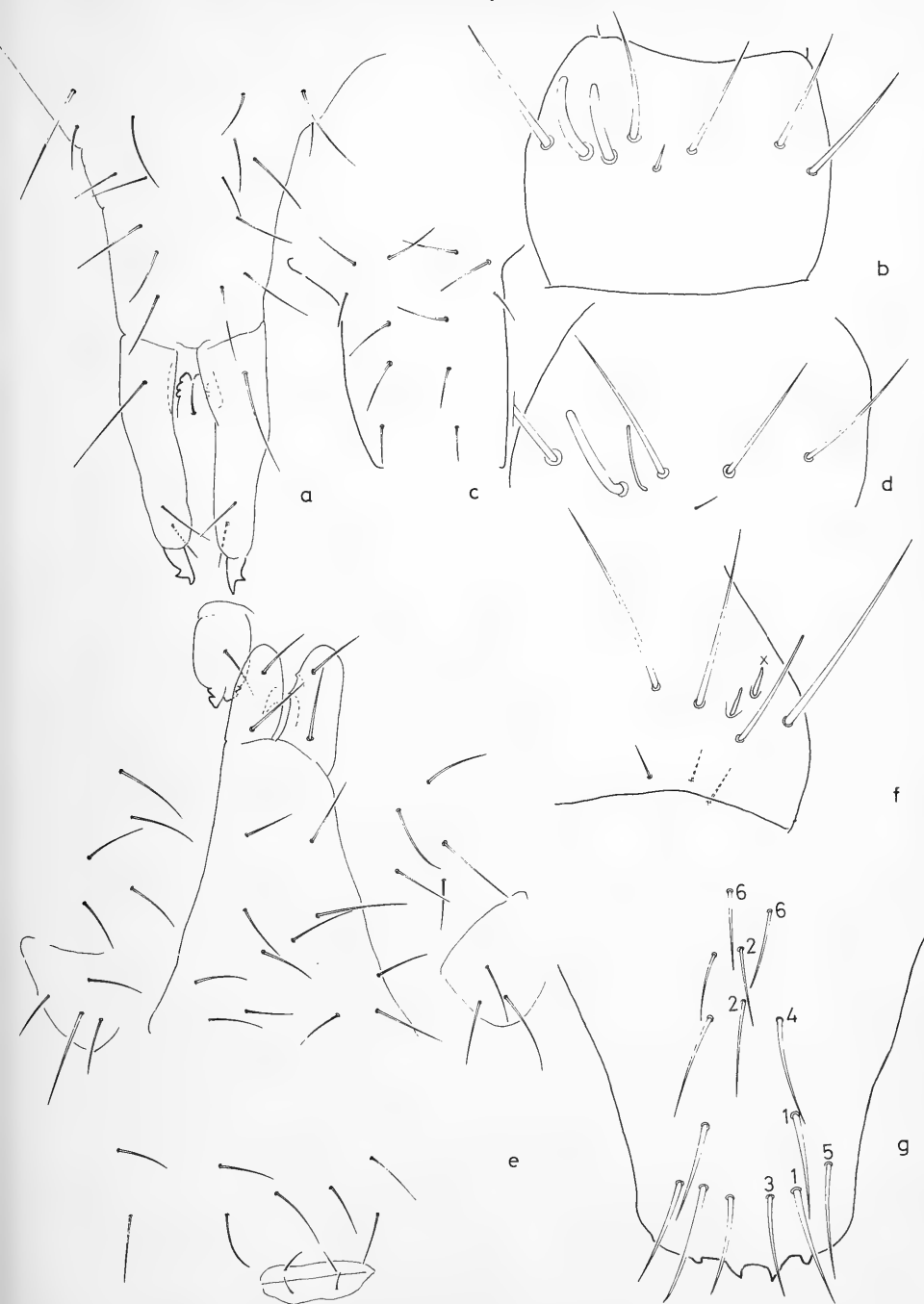


Fig. 32. *Tetracanthella* cf. *hygropetrica* Cassagnau, 1954. a, posterior face of furca and retinaculum. *Folsomides parvulus* Stach. b, ventral face of ant<sub>1</sub>; c, manubrium of holotype. *Folsomides nanus* Ellis. d, ventral face of ant<sub>1</sub>; e, ventral aspect of abd<sub>1-5</sub>. *Folsomia ksenemani* Stach. f, ventral face of ant, (sensilla indicated by x is absent in smaller immatures); g, chaetotaxy of anterior face of manubrium, with indication of the order of appearance of the setae in the ontogeny

and small adults. Posterior face of dens with 3 + 3 setae, except in three specimens (two juveniles from sample 16, and a ♀ from sample 30) in which I found only 2 + 3.

Dr. A. Szeptycki kindly loaned me the holotype of the species under consideration. It is mounted on a slide bearing two labels, both with a blue margin and handwriting: a small one stating "Unicum", and a larger one "*Folsomides parvulus* n.g.-n.sp. Berekalja 1915". The specimen is an adult ♀ and measures 590 µ. The condition is rather poor, but I could study the furca in some detail. The dens has at one side distinctly 3 setae; in the other dens the two distal setae are visible, but due to a dirt particle observation of the basal seta is impossible. The posterior face of the manubrium bears 6 + 6 setae (Fig. 32c).

Again, the species seems to be parthenogenetic.

### **Folsomides americanus** Denis, 1931

Material: sample 13: 1 ♀ and 1 juv.; 26: 4 ♀ and 1 juv.; 27: 3 ♀ and 6 juv.; 43: 4 juv.

Discussion. The difference between *americanus* and *parvulus* is based on one character only. The posterior pair of ocelli is lost in *americanus*. Not only pigment granules but also a lens are missing, and the primary granulation on the location of the second pseudocellus in *parvulus* is completely regular.

After some hesitation (due in part to the apparent coexistence of *americanus* and *parvulus* in sample 43), I prefer to separate *americanus* as a distinct species. One of the arguments for doing so is that *parvulus* shows no trend indicating obliteration of the posterior ocellus: posterior and anterior ocellus always show an almost equally dense pigmentation and are equally large; moreover, there are no asymmetries.

The ocelli of many immatures of *americanus* are not or only weakly pigmented, as in *parvulus* and "*anophthalmis*" Hepburn & Woodring, 1964.

Although the limited number of specimens does not permit of definite statements, here too there is an indication of parthenogenesis.

The species seems to occur in all subtropical regions in the Americas and Europe. It has already been recorded from the Lebanon (Cassagnau & Delamare Deboutteville, 1955), Spain (Selga, 1973), and France (Cassagnau & Rouquet, 1962).

### **Folsomides navacerradensis** Selga, 1962

Material: sample 36: 4 ♀, 5 ♂, and 11 juv.

Discussion. The specimens agreed well with the description by Selga, apart from the variability in dental chaetotaxy, as described by Petersen (1965). The number of setae on the posterior face of the manubrium fluctuated (in adult specimens) between 7 + 7 and 12 + 12; on dentes both 3 and 4 setae occurred. The Cretan material thus cannot be related to *F. navacerradensis pratensis* Palissa & Živadino-  
vić, 1974, from Bosnia. Here, only 3 setae are constantly present on the dens, and

the manubrium has at most 8 pairs of setae. In two specimens (a juvenile and a ♂) one of the dentes lacked the mucro. This is the distinctive feature of *F. meridionalis* Dallai, 1973, described from the Eolic Islands.

***Folsomides marchicus* (Frenzel, 1941)**

Material: sample 24: 2 ♀.

The specimens did not deviate from the original description. Pigment was fairly well developed; posterior face of dens with 3 + 3 setae in both specimens.

The species has been recorded before from Spain and Ibiza, France, Italy, Germany, Switzerland, the ČSSR, and Yugoslavia.

***Folsomides nanus* Ellis, 1974 (Fig. 32 d, e)**

Material: sample 12: 2 ♀ and 1 juv.; 25: 1 ♀; 30: 2 ♀; 36: 18 ♀ and 2 ♂; 43: 2 ♀, 3 ♂, and 3 juv.; 45: 16 ♀, 6 ♂, and 4 juv.

Discussion. Mean length of the females 0.70 mm ( $s = 0.08$ ,  $s_{\bar{x}} = 0.01$ ,  $n = 41$ ), that of the males 0.55 mm ( $s = 0.04$ ,  $s_{\bar{x}} = 0.01$ ,  $n = 11$ ). The specimens are in good agreement with the material of *nanus* from Rhodes, with one exception. The dens shows no trace of a mucro and is very blunt in the ventral view. In the material from Rhodes, the dens is always more or less contracted apically to a vestige of a mucro in the ventral view. Moreover, in the present material the manubrium has at its posterior face a slightly higher number of setae, the modal value being 6 + 6, often asymmetrically 5 + 6 or 6 + 7 (Fig. 32 e).

Since the Cretan material was collected in the autumn, seasonal variation may partially explain the difference, and I therefore refrain provisionally from giving the Cretan material subspecific status.

***Folsomia ksenemani* Stach, 1947 (Fig. 32 f, g)**

Material: sample 12: 2 juv.; 13: 33 juv. (2 immature ♀); 14: 3 juv.; 19: 10 juv. (1 immature ♀); 21: 1 juv.; 25: 39 juv.

Discussion. The number of ocelli is constantly 1 + 1, and I have no reason to agree with Christiansen (1959) and other authors that *ksenemani* represents aberrant one-eyed specimens of a two-eyed species such as *penicula* Bagnall, 1939.

In the antennal organ I, two small sensillae (but in the smaller immatures constituting the majority of the present material only one) are guarded by a sense hair which is barely differentiated from a normal hair (Fig. 32 f). Moreover, a small basal spine is present here; the dorsal homologues being two comparable spiniform setae. Thoracal sternites without setae. Ventral tube anteriorly bare, posteriorly usually with 4 setae, in lateral flaps usually with 3 + 3, sometimes with 3 + 4 and in one example even with 4 + 4 setae. All this applies to immature material.

The number of setae on anterior face of manubrium varied strongly. Table 6 gives the frequencies I could observe. Although the present material includes no mature specimens, the higher setal numbers already outvalue the limit given by

Table 6. Number of anterior setae of the manubrium of *Folsomia ksenemani*

Sample nr.	Number of setae											
	4	5	6	7	8	9	10	11	12	13	14	15
12	-	-	-	-	-	-	1	1	-	-	-	-
13	-	-	3	2	3	5	7	4	7	-	1	1
14	-	-	-	-	1	-	1	1	-	-	-	-
19	1	-	2	1	1	1	2	-	2	-	-	-
21	-	-	-	1	-	-	-	-	-	-	-	-
25	-	-	-	-	2	4	3	4	21	2	3	-
Total	1	-	5	4	7	10	14	10	30	2	4	1

Stach (1947) for *ksenemani*, and consequently the material should be identified as *F. pseudodiplophthalma* Stach, 1947. These two species have, however, been synonymized on rather convincing grounds by Poinso (1972). Acting furthermore as "first revisor", she has invalidated *pseudodiplophthalma*, and I follow her in the synonymy. The low values are, however, no less instructive, because they suggest an impending synonymy of *ksenemani* with (the senior name!) *monophthalma* Bagnall, 1939, described from Romania, and, according to Lawrence (1973) an immature! Topotypical material might show that this suspicion is justified.

The gradual rise in setal number on the manubrium follows a rather regular pattern. In Fig. 32 g I have numbered the setae according to the order in which they appear. Only level 4 and 5 are interchangeable, and I often found a specimen with both arrangements asymmetrically.

### ***Cryptopygus thermophilus* (Axelson, 1900)**

*Isotomina salaymehi* Christiansen, 1959. — **nov. syn.**

Material: sample 4: 3 ♀, 3 ♂, and 6 juv. + 10 ex. in alcohol; 7: 2 ♀, 6 ♂, and 3 juv.; 18: 1 ♀ and 5 juv.; 20: 1 ♀, 1 ♂, and 10 juv.; 32: 1 juv.; 41: 2 ♀ and 2 juv. + ca. 90 ex. in alcohol; 48: 3 ♀, 1 ♂, and 2 juv. + 100 ex. in alcohol.

Discussion. The unguis is toothed in almost all specimens. Tenent hairs not clavate. Proportional width of postantennal organ rather variable. Ventral tube with 4+4 setae on lateral flaps, and 1+1 posterior setae. Thoracic sternites without setae.

The species described by Christiansen, recorded from several localities in the Lebanon, would differ from *thermophilus* by a pair of blunt sensory setae on abd<sub>6</sub>, a faint subdivision in the distal part of the tibiotarsus, a small ocellus D, and by having the longest setae on the abdomen three times longer than shortest ones. All these characters can be found in material referable to *thermophilus*, not only in the present material, but also in specimens from western Europe. The sensory hair of abd<sub>6</sub> is typical for the whole species group.

The species seems to be cosmopolitan.

### ***Cryptopygus ponticus* (Stach, 1947)**

Material: sample 9: 1 juv.; 10: 1 ♀ and 6 juv. + 68 ex. in alcohol; 11: 1 ♀, 5 ♂, and 2 juv. + 23 ex. in alcohol; 16: 1 ♂; 17: 3 juv.; 23: 4 juv.; 29: 1 ♀, 1 ♂, and 2 juv.;



30: 1 ♀ and 2 juv.; 34: 1 ♀ and 1 juv.; 36: 1 ♀ and 2 ♂; 37: 2 ♀; 38: 1 ♀; 41: 1 ♀, 1 ♂, and 1 juv.; 42: 1 ♂ and 5 juv.; 43: 2 ♂ and 8 juv.

Discussion. Tooth on internal unguual lamella distinct. Lateral flaps of ventral tube constantly with 4+4 setae. Posterior face of ventral tube in adult specimens always with more than 1+1 setae: modal value 2+2, less frequent values 1+2 or 2+3. (This is a useful additional difference from *C. thermophilus*, but may not be valid everywhere, since Yosii (1966b) described *ponticus* from Afghanistan with 1+1 posterior setae). Juveniles often have only 1+1 posterior setae; in adults the longest, distal setae seem to be the homologues of the pair present in *C. thermophilus*.

### ***Cryptopygus triglenus* n. sp. (Fig. 33)**

Material: sample 23: 2 juv.; 26: 5 ♀, 5 ♂, and 3 juv.; 27: 5 ♀ and 5 juv.; Holotype is a ♂ from sample 26.

Description. Mean length of the 5 males 0.76 mm ( $s = 0.03$ ,  $s_x 0.01$ ), that of the 10 adult females 0.92 mm ( $s = 0.08$ ,  $s_x 0.03$ ).

Pigment sparsely distributed in grey clouds over head and body; eye patches are well pigmented. Integument finely and regularly granulate. Hair cover consists of moderately fine smooth setae.

Ant: Head = 1.08. Ant. 1:2:3:4 = 36:54:57:100. Ant<sub>4</sub> without apical retractile bulb, only a semiglobular protuberance; subapically, a small sensilla in a deep groove, guarded by a short strongly bent seta; the segment is covered by normal hairs and by many sense hairs. Ant<sub>3</sub> with ant. org. III composed of two flexed sensillae guarded by two sense hairs; external sensilla in the middle of this segment spine-like (Fig. 33 d). Antennal organ I with two long sense hairs, the external one the shortest, and a small spine-like setula near base of segment (Fig. 33 e).

Eyes 3+3. Two ocelli set close together in one intense pigment spot, a third one lies about 1.5 eye-diameters more caudad, on its own pigment bed. Postantennal organ oval, with a thickened anterior "rim" and a weak transverse subdivision (Fig. 33 b). Labral chaetotaxy 4/5, 5, 4. Mandible normal, maxillar head with rather narrow lamellae which do not reach beyond the claw.

Thoracal sternites without setae. Unguis with a distinct inner tooth, without lateral or dorsal teeth; unguiculus with weak inner lamella, without apical filament (Fig. 33 f). No clavate tenent hairs. Apical part of tibiotarsus weakly separated from main part by indistinct furrow.

Abdominal sternites in mid-line bare. Ventral tube without anterior setae, posteriorly with about 2+2 setae (the distal pair the strongest), in lateral flaps with 4+4 setae. Retinaculum quadridentate with 1 seta on corpus. Male and female genital orifices normal. Abd<sub>5</sub> and abd<sub>6</sub> completely fused. On abd<sub>6</sub> ventrolaterally, an indistinct sense hair.

Manubrium anteriorly with 1+1 strong subapical setae, posteriorly with about 20+20 setae in a very symmetrical arrangement (Fig. 33 a). Two pairs of manubrial spines. Dentes finely corrugated, anteriorly with 15 strong setae, posteriorly with 1, 1, 1, 2, 2 fine setae (Fig. 33 c). Mucro bidentate, not lamellate.

Discussion. As far as I know, the genus includes only two species with 3+3 eyes:



Fig. 33. *Cryptopygus triglenus* n. sp. a, posterior chaetotaxy of manubrium; b, eye-patch and postantennal organ; c, posterior and anterior aspects of mucrodens; d, antennal organ III; e, ventral aspect of ant<sub>1</sub>; f, claw of P<sub>3</sub>.

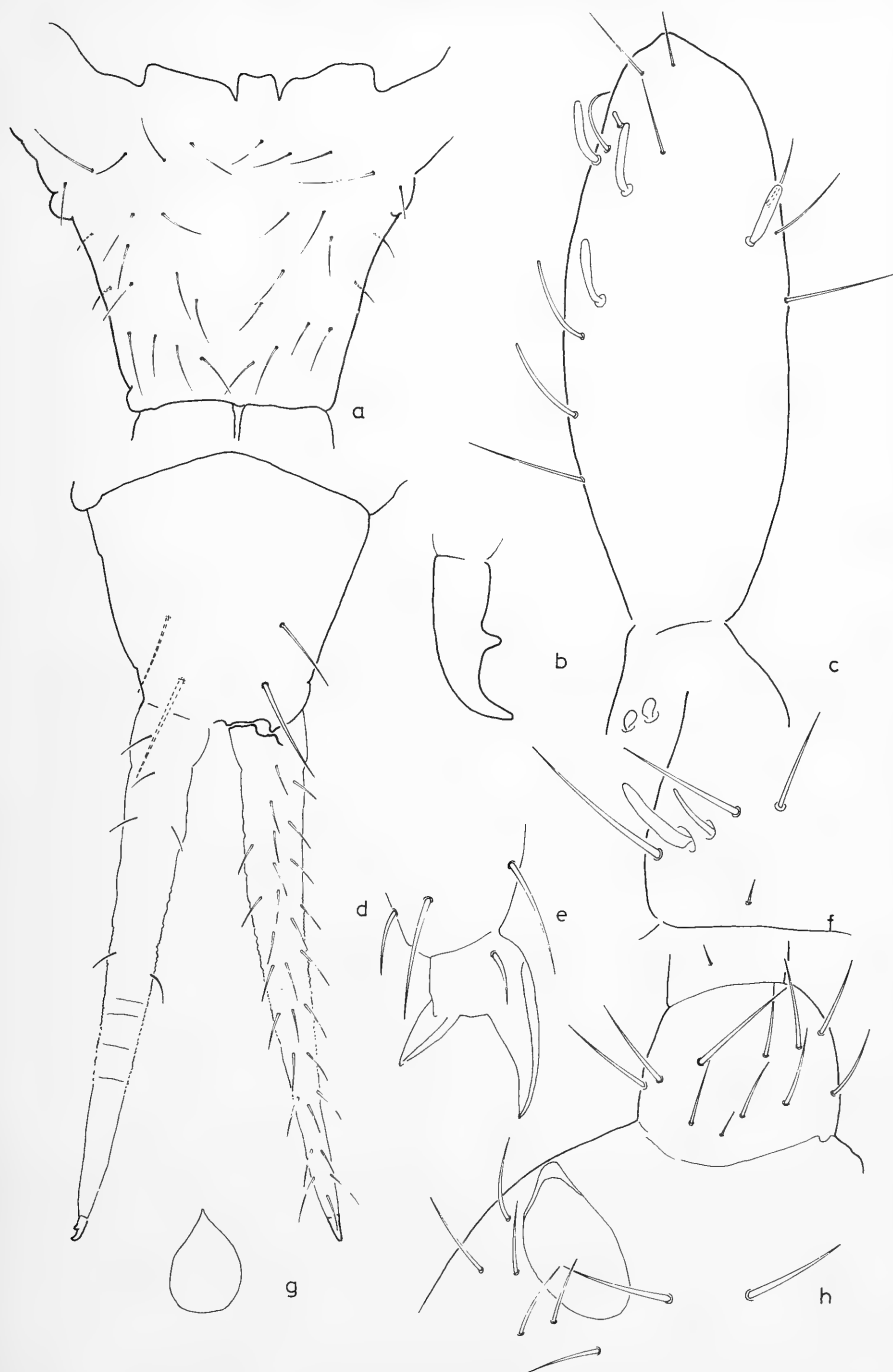


Fig. 34. *Cryptopygus debilis* (Cassagnau). a, posterior aspect of manubrium; b, mucro; c, location of sensillae and some setae on ant<sub>4</sub>; d, anterior aspect of manubrium, posterior (left) and anterior face (right) of mucrodens; e, claw of P<sub>3</sub>; f, antennal organ I; g, receptaculum seminis; h, dorsal aspect of postantennal organ and ant<sub>1</sub>.

*C. trioculatus* Izarra, 1972, from Argentina, and *insignis* Massoud & Rapoport, 1968, from Patagonia. The former belongs to the series with the dens much reduced (anteriorly only one, posteriorly two setae) and is undisputedly very different from *triglenus*. *C. insignis*, however, comes close to *triglenus*, but differs in the tridentate mucro and the somewhat shorter dens with a different chaetotaxy, especially posteriorly, and, finally, in the enormous postantennal organ.

*C. triglenus* obviously is a near relative of *C. ponticus*, and differs from that species only in its eye number. It is not without some hesitation that I propose this new species on the basis of a single difference. That for the time being I nevertheless consider *triglenus* a good species is explained by the fact that no intermediate eye numbers (3+4, 4+4 or 4+5) have been detected in the rich material available.

The specific name means "with three jewels".

### **Cryptopygus debilis** (Cassagnau, 1959) (Fig. 34, 35 a, b)

Material: sample 13: 1 ♀ and 12 juv.; 14: 2 juv.; 25: 6 juv.; 35: 6 ♀; 36: 1 juv.; 44: 16 juv.; 45: 1 ♀ and 1 juv.

Description. *Isotomina debilis* was described from the Central Pyrenees, from two alpine localities. This makes my identification less likely. It is unfortunate that the original description is very short, and I add, therefore, a complete description of my material here.

Mean length of the 7 adult females 0.53 mm ( $s = 0.02$ ,  $s_{\bar{x}} = 0.01$ ). No trace of pigment. Integument basically normal, with a fine primary granulation. However, abd<sub>4</sub> and abd<sub>5-6</sub> show numerous, irregularly distributed circular structures which I cannot interpret (Fig. 35a). They are about as large as hair bases, sometimes smaller, and consist of a raised ring with a depressed centre — resembling an erythrocyte. They occur in juveniles and adults, and are not correlated with moulting. I would consider this phenomenon to be an artefact if it was not always limited to the same segments and did not occur in material from all localities. I have never seen a comparable structure, save perhaps in entomobryoid pseudopores. Hairs normal, smooth.

Antennae: head = 1.2; ant. 1:2:3:4 = 30:50:55:100. Ant<sub>4</sub> without exsertile papilla, subapical sensilla remarkably large, guarded by an equally proportionally strong, bent hair. Some sense hairs, difficult to identify, occur on this antennomere, as well as 3 outer and 1 inner swollen, curved sense hairs (Fig. 34c). Ant<sub>3</sub> with antennal organ III composed of two short sensillae, guarded by two apparently normal hairs. External sensilla of this antennomere in the shape of a curved spine. Antennal organ I consists of a thick outer and a thin (and a bit shorter) inner sense hair (Fig. 34f).

Eyes absent. Postantennal organ usually very large, almost without a rim (only some thickening in ventral corner). Some specimens (juveniles) have, however, a somewhat less disproportionate PAO. Mouth parts normal. Labral chaetotaxy is 3/5, 5, 4.

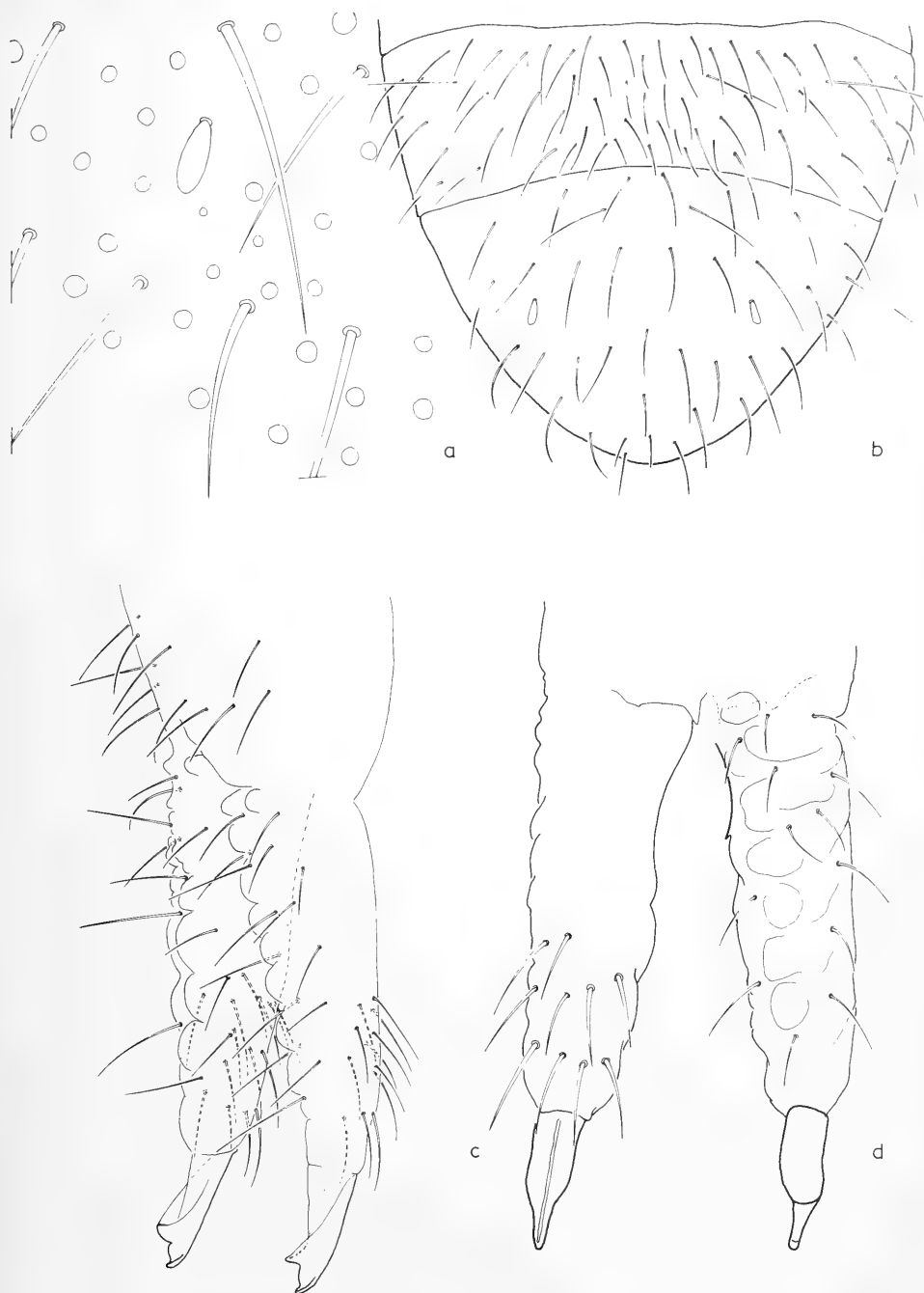


Fig. 35. *Cryptopygus debilis* (Cassagnau). a, sensilla, some setae, and cuticular ornamentation of abd<sub>3</sub>; b, chaetotaxy of abd<sub>4-6</sub>. *Clavisotoma albertinae* n. sp. c, lateral aspect of furca; d, anterior (left) and posterior (right) aspect of mucrodens

Thoracal sternites bare except 1 + 1 seta on  $th_3$ . Claws simple, unguis without teeth, unguiculus with proportionally strongly developed outer lamella, tenent hairs not clavate; subsegmentation of tibiotarsi not seen (Fig. 34e).

Ventral tube anteriorly without setae, 4 + 4 setae on lateral flaps, posteriorly usually with 1 + 2 setae (if more adult material had been available this might have been a higher figure). Retinaculum quadridentate, with one seta on corpus. Abdominal sternites bare in median line.

Manubrium posteriorly with about 16 + 16 or 17 + 17 setae (Fig. 34a), anteriorly in all except two adult specimens with 2 + 2 setae, arranged in a distal pair and another pair in about the middle of the manubrium (Fig. 34d). The same arrangement was found in only one juvenile. The remaining juveniles and one adult had only the distal pair of setae. The last adult specimen, which was at the point of ecdysis, had 1 + 1 setae on the old skin, and 2 + 2 on the new one.

Manubrium distally with a pair of weak though distinct manubrial spines (Fig. 34a). Dentes posteriorly with about 25 corrugations, basal and apical part not corrugated (Fig. 34d). Anteriorly there are about 30 setae, posteriorly 1, 1, 2, 2 fine setae. Mucro bidentate (Fig. 34b).

Abdomen 5 and 6 completely fused.  $Abd_5$  with 1 + 1 short clavate sensillae. They are usually relatively very thick, but in some cases are slightly more slender (Fig. 35a, b).

Since part of the juvenile material consisted of immature males, there is no question of regarding the species as parthenogenetic.

Since Mr. P. N. Lawrence is preparing a revision of the genus *Cryptopygus*, I leave it to him to compare this species with the other members of the genus.

### ***Proisotoma minuta* (Tullberg, 1871)**

Material: sample 4: 1 ♀; 6: 1 ♀; 23: 1 ♀, 1 ♂, and 2 juv.

The species seems to have an almost cosmopolitan distribution.

### ***Ballistura schoetti* (Von Dalla Torre, 1895) (Fig. 37f)**

Material: sample 40: 1 ♀ and 16 juv.; and also some 120 specimens, apparently all immatures, in alcohol.

The only adult specimen measured 1.0 mm, and was still very pale. This halophilous species is distributed along the coasts of the Atlantic and the Mediterranean.

### ***Clavisotoma albertinae* n. sp. (Fig. 35c, d, 36, 37a-e)**

Material: sample 26: 4 juv.; 32: 15 ♀, 13 ♂, 3 juv., and 1 specimen of unknown sex; 36: ca. 550 ex. in alcohol; 37: 1 juv.; 38: 10 ♀, 11 ♂, 11 juv., and ca. 50 ex. in alcohol; 39: ca. 300 ex. in alcohol, not sorted according to sex; from 43: 1 ♀; 50: 1 ♀. All material (except the specimens in alcohol) mounted individually on slides in Marc André II; some specimens depigmentated. Holotype is a ♂ from sample 32, all other specimens being paratypes except a very immature specimen from 32, which cannot be attributed to the species with sufficient certainty.

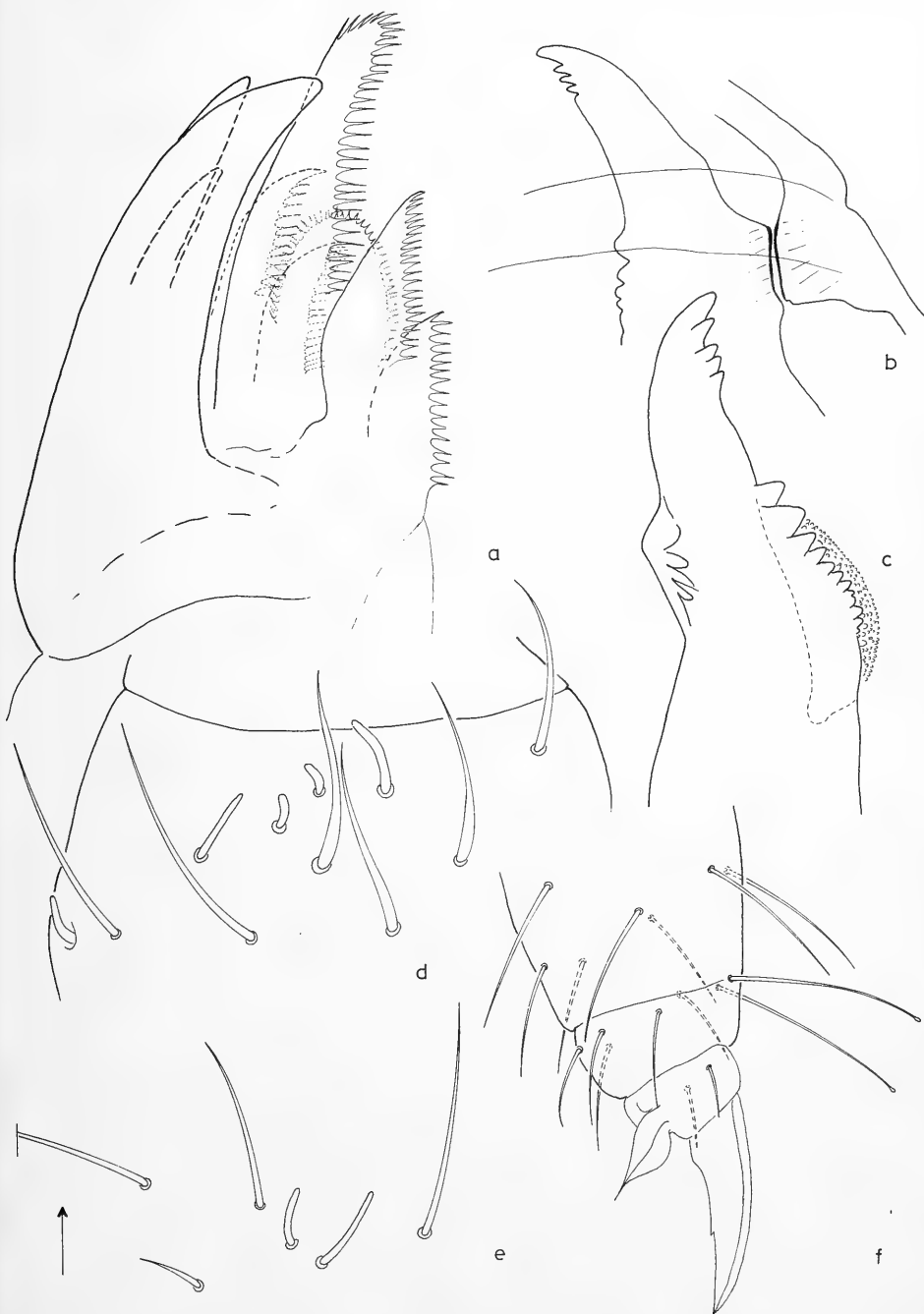


Fig. 36. *Clavisotoma albertinae* n. sp. a, maxillar head; b, articulation of mandible against the clypeus; c, mandible; d, antennal organ III; e, antennal organ I; f, claw of P<sub>2</sub>

Description. Total length 1.1 mm, the sexes not differing markedly in size. Habitus stout, characteristic for the genus. Pigmentation moderate, bluish-grey. The whole body and all the extremities are pigmented; head and dorsum distinctly darker than other parts. Integument smooth, hairs short and stout, curved. Antenna: head = 0.85. Ant. 1:2:3:4 = 45:48:60:100. Ant<sub>4</sub> without apical papilla, but with a small subapical globule in a deep pit. Antennal organ III consists of two short blunt and strongly curved rods, guarded by two also proportionally rather short and blunt sense hairs. Another short and curved sensilla at outer surface of same segment (Fig. 36d). Antennal organ I (ventrally on ant<sub>1</sub>) composed of two comparatively long blunt sense hairs and a short but otherwise seemingly normal hair (Fig. 36e). Eyes 8 + 8, all well developed though not all equally large (G and H are smaller), in a black eye patch (Fig. 37b). Postantennal organ shortly oval, with an irregular, sometimes rather thick rim; its longest axis is about as long as the diameter of ocellus B (Fig. 37e).

Labral chaetotaxy 2/5, 5, 4. Mandible stout, but essentially normal for the family, with a strongly chitinized outer condyle (Fig. 36 b, c) which is apposed to the interior surface of the clypeus. Maxilla essentially typical with large, three-toothed claw, globular body, and two dorsal and two ventral fringed lamellae, which seem to have a tendency to split (Fig. 36a).

Tibiotarsi of P<sub>1</sub> with one, those of P<sub>2-3</sub> with two clavate tenent hairs. Unguis with distinct inner tooth, without lateral or dorsal teeth. Unguiculus with strongly curved inner lamella, tapering to an apical filament (Fig. 36f). Thoracic sternites bare.

Ventral tube with 4 + 4 setae on lateral flaps, and 1 + 1 posterior setae (Fig. 37d). Retinaculum tridentate, with 1 seta on corpus (Fig. 37c). Abdominal sternites bare.

Manubrium anteriorly bare, posteriorly with many (40-60) setae. Antero-distally a pair of strongly sclerotized acute manubrial hooks (Fig. 37a). Anterior face of dens with a large, somewhat variable number (8-15) of setae in distal half; posterior face with about 13 setae and the bosses characteristic for the genus. Mucro typical for the genus, large, two-toothed, strongly lamellate (Fig. 35c, d). Male genital orifice on a tubercle surrounded by a dense row of about 30-40 fine hairs.

Discussion. An inspection of the synoptic key I prepared for *Clavisotoma* (Ellis, 1970), shows that a combination of characters: presence of tooth on the unguis, 8 + 8 eyes, tenent hairs 1, 2, 2, retinaculum tridentate, terminal filament present, has not previously been found in this genus. *C. albertinae* is furthermore highly characteristic by virtue of the large number of setae occurring antero-distally on the dens. *C. albertinae* seems most closely related to *hankoi* (Stach, 1930), described from Hungary and recorded from Switzerland (Gisin, 1960).

In Márathos (samples 37, 38, 39) we witnessed a true mass occurrence of this species, albeit limited to only 20-30 square metres (as far as could be explored), where countless numbers were walking about on the almost bare, moist clay of a piece of waste land and on stones lying at its edge. We presume that the animals had been (dormant?) living deep in the soil during the dry season, and came to the





Fig. 37. *Clavisotoma albertinae* n. sp. a, manubrium-dens junction; b, eye patch; c, retinaculum; d, ventral tube; e, postantennal organ and anterior ocelli. *Ballistura schoetti* (Von Dalla Torre). f, ventral aspect of ant., *Dimorphotoma porcellus* n. sp. g, maxillar head; h, lateral aspect of mucrodens; i, ventral aspect of mucrodens; j, claw of  $P_3$

surface — or were actually even driven to the surface — by the soaking and swelling of the clay of the subsoil after the torrential rains of the last few days.

It is a pleasure for me to dedicate this species to my wife Albertine, who not only participated actively in the collecting but also has the gifted collector's knack of finding unusual things in unexpected places. It was she who discovered the mass occurrence of the species under consideration.

***Dimorphotoma porcellus* n. sp. (Fig. 37 g-j, 38, 39, 40 a-d)**

Material: sample 25: 7 ♀ and 1 ♂; 26: 93 ♀ and 69 ♂; 27: 1 ♀; 28: 9 ♀ and 19 ♂. Moreover as alcohol material, not sorted according to sex, about 700 specimens from sample 26. Holotype is a ♂ from sample 26.

Description of female. Total length 1.4 mm (sd = 0.11 mm, n = 12). Habitus stout, about as in *Clavisotoma*. Pigmentation sparse: greyish-blue pigment tinges (without strong concentrations or mottlings) the whole dorsal part of the body, especially the thoracic tergites, and the extremities. Only the enveloping cells around the internal part of the eyes are strongly pigmented. Integument smooth, primary granulation very fine, except in the "crown" on abd<sub>5</sub> (see below). Hair cover dense, consisting of fine, smooth acute setae, only on abd<sub>5-6</sub> a bit longer, and sometimes with a few serrations at anterior face; some special setae around the "crown".

Abd<sub>5</sub> well separated from abd<sub>6</sub>. Seen from above, abd<sub>6</sub> seems fairly small due to pronounced cryptopygy.

Ant/head ratio is 1.05. Ant 1:2:3:4 = 42:65:66:100. Ant<sub>4</sub> without apical exsertile papilla, but with a slender spine-like sensilla subapically, a small curved sensilla in a shallow groove, many seemingly normal hairs, and dorso-apically (ca. 20) slender curved hair-like but blunt sensillae. Ant<sub>3</sub> with ant. org. III consisting of two small bent sensillae flanked at both sides by a somewhat larger almost straight hair, furthermore a sensilla in the middle of outer face (Fig. 40d); ant<sub>2</sub> with normal setae, one very slender curved blunt sense hair apically in latero-ventral position, and proximo-ventrally as well as proximo-dorsally, a very fine and short hairlet; ant<sub>1</sub> somewhat swollen, proximo-dorsally with a fine setula, ventrally with antennal organ I consisting of a fine sense hair, a shorter curved sense hair, and a short sensilla between them (see Fig. 40b).

Antennal bases swollen, bare; the frontal region seems somewhat jammed between the antennal bases, the hairs pointing in all directions (Fig. 39a). PAO broad-oval, twice as long as diameter ocelli A or B, mostly simple but sometimes with a constriction in the middle of its long axis. Ocelli 8+8, all except G and H equally large (Fig. 39a). Labral chaetotaxy 2/5, 5, 4, distal two rows on low papillae (Fig. 40c). Labium normal; labial palp, see Fig. 39b. Mandible normal for the family (see drawing of *Clavisotoma albertinae*, Fig. 36c). Maxilla also normal, with tridentate claw, globular body, and 2+2 lamellae which do not reach beyond the apex of the claw (Fig. 37g).

Feet 1, 2, 3 with 1, 2, 2, weakly clavate tenent hairs. Unguis without inner of lateral teeth. Unguiculus about 0.5 times unguis, blunt, without apical filament (Fig. 37j). Thoracic sternites 1 and 3 bare, that of th<sub>2</sub> with 1+1 seta.

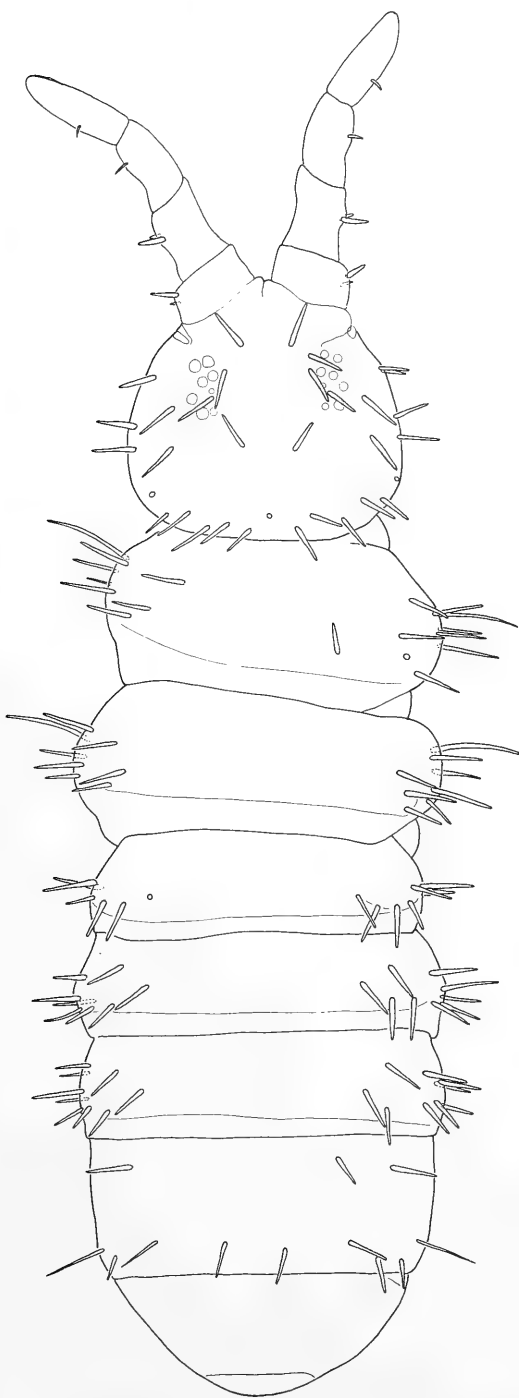


Fig. 38. *Dimorphotoma porcellus* n. sp., habitus of a male

Ventral tube anteriorly without seta, laterally with 4 + 4, posteriorly with 5 + 5 or 6 + 6. Abdomen ventro-medially without setae. Retinaculum tridentate, with one seta on corpus.

Manubrium: dens: mucro = 10: 6: 1. Furca moderately long, reaching to the distal border of abd<sub>2</sub>. Manubrium anteriorly with 1 + 1 (seldom 1 + 2) distal setae, posteriorly with many (maximally about 30 + 30) setae, leaving a medial stripe bare. Manubrium-dens junction with two low cushion-shaped ridges (Fig. 39c). Dens anteriorly only distally with 1, 1, 2 setae, posteriorly with a variable number (about 6) of ill-defined humps and 7 setae. Mucro proportionally short, bidentate, lamellate (Fig. 37h, i).

Dorsally on abd<sub>3</sub> there is a rosette shaped like a head of lettuce. It consists of strongly crisped integument that is relatively coarsely grained (granulation visible at x 400). The hairs in this vicinity are longer and more slender and bent than the normal body hairs (Fig. 39e, f).

Female genital orifice of two strongly protruding lips, each having 1 + 1 normal seta, i.e., almost as long as setae anterior and posterior to the genital orifice. Spermatheca not seen.

Description of the male (Fig. 38).

The male is distinctly larger than the female: mean size of 18 random specimens was 1.6 mm ( $s = 0.15$ ). But the essential difference, very striking even at low magnifications, is the possession by the males of a large number of strong yellow spines on antenna, head, thorax, and abd<sub>1-4</sub>. Moreover, the hair cover on abd<sub>3</sub> and the expression of the rosette are different, and the antennae are aberrantly shaped.

Ant<sub>4</sub> is roughly normal in shape, differs only in the possession of one small, slightly hook-like spine in lateral position. Ant<sub>3</sub> is somewhat thickened and has a slightly oblique base, and also one lateral spine, which is a bit curved. Ant<sub>2</sub> is distinctly thickened and has two spines of different length, as has ant<sub>1</sub>. Ant<sub>1</sub> is even more inflated than ant<sub>2</sub>, and the antennal sockets are correspondingly enlarged.

The spines on head and body are essentially aligned along the lateral parts. Although asymmetries and anomalies do occur (e.g. the vertical pair on the head is often absent), the arrangement is essentially a very orderly one. The spines are replaced on abd<sub>3</sub> by strong, straight macrochaetae (sometimes having a few serrations).

The rosette on abd<sub>3</sub> is much less distinct in the male than in the female, and the integument lacks the coarse texture occurring in that sex. The setae on abd<sub>3</sub> (and to a lesser extent also those on abd<sub>6</sub>) in the discal area, i.e., close to the rosette, are strongly protracted to a wavy thread, terminating in a tiny globule (Fig. 39d).

The male genital orifice is a large cone, encircled by about 20 setae; papilla bearing 4 + 4 setae (Fig. 40a). Vas deferens visible in a few specimens only.

Discussion. Leaving aside sexual dimorphism, the new species comes close to *Clavisotoma* Ellis, 1970, especially because of the hump structure of the dens. However, the pair of setae antero-distally on the manubrium argues against such a relationship. Otherwise, the resemblance to the littoral *Proisotoma buddenbrocki* Strenzke, 1954, is rather striking. It is unfortunate that no submature males are present in the material, making it impossible at present to say whether the secondary sexual traits are obtained gradually or not.

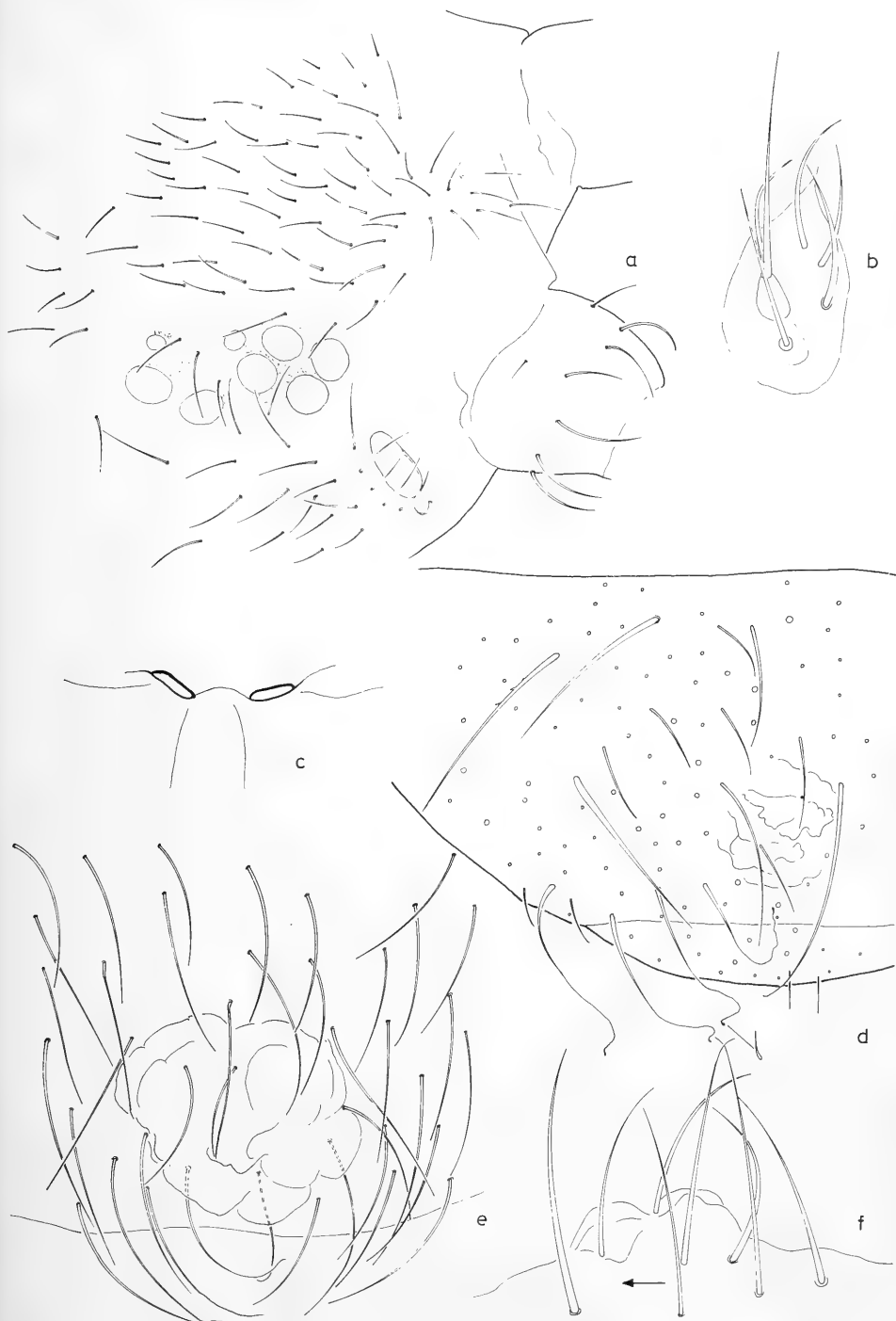


Fig. 39. *Dimorphotoma porcellus* n. sp. a, ♀, frontal region of head in latero-dorsal aspect; b, palpus and lobus externus; c, manubrium-dens junction; d, dorsal aspect of abd<sub>3-6</sub> of a male, showing chaetotaxy (only some setae drawn) and the rosette; e, dorsal view of abd<sub>5</sub> of a female; f, rosette of a female in lateral view

Sexual dimorphism on the scale described here is not common in the Isotomidae. A comparatively low degree of dimorphism occurs in *Proisotoma papillosa* Stach, 1937, *Hydroisotoma schaefferi* (Krausbauer, 1898), and *Australotomurus echidnus* (Womersley, 1934). A really strong sexual dimorphism is known to occur in only three instances (which are, however, not undisputed — cf. Goto, 1972): *Guthriella* Börner, 1906, *Rhodanella* Salmon, 1945, and *Dimorphotoma* Grinbergs, 1975 (*Dimorphiella* Grinbergs, 1968, nec Valkanov, 1928). *Guthriella* is much too specialized to be compared with the present species. *Rhodanella*, with only the species *R. minos* (Denis, 1928), is considered by Goto (1972) a possible ecomorph of *Proisotoma stachi* Goto, 1957, although the evidence he gives is not very decisive, and there is no explanation as to why the ecomorphosis would affect only one sex. However this may be, both the type of sexual differentiation (a pair of large horns on the male head, as well as a number of strong but not spiniform body setae) and the female or submature male morphology exclude a close affinity between *Rhodanella minos* and *porcellus*. Note that Denis originally placed *minos* in *Vertagopus*.

Even the similarity to *Dimorphotoma muriphila* (Grinbergs, 1968) is not very strong. In that species the antennae are not affected by the sexual dimorphism, and the rosette on abd<sub>5</sub> with its accompanying specialized setae is not present. Moreover, in *muriphila* abd<sub>4</sub> is strikingly longer than abd<sub>3</sub>. Less important differences with respect to *muriphila* concern the occurrence in this species of spines in the male not only dorso-laterally but also dorso-medially, and also on abd<sub>5</sub>. Finally, *muriphila* has a tridentate mucro. Still, although I cannot exclude the possibility that by including *porcellus* in *Dimorphotoma* I am making the genus polyphyletic, I think it better not to create a new genus for *porcellus* at present.

The specific name, which means a sucking-pig, refers not only to the plump habitus but also to the roast pig for which Drosiá, the type locality, is widely and rightly renowned.

The species occurred very locally, and in enormous numbers. Very many specimens were seen walking, apparently erratically, on the ground and on large boulders. The collecting date was just after some days of heavy autumn rains, which had thoroughly soaked the loamy subsoil. This and the fact that the material seems to be composed exclusively of adults suggest that the specimens had passed the period of summer drought in the subsoil, and had been driven to the surface by the inundation of their summer resort. Two findings are relevant here: first a comparatively large percentage (in the order of 10%) of the specimens were infected by Sporozoa; and second, the genital area was conspicuously dirty, and I had some difficulty in finding a specimen suitable for a drawing of the male genital papilla. I should also mention that active testicular tissue, which is usually clearly visible even in cleared specimens, could not be found, and the same holds for spermathecae and a distinct vas deferens. In almost all specimens the intestine was full (unidentifiable, mainly amorphous material). My suggestion is that, synchronized as they were by the weather conditions, the specimens had not yet passed through their moult to the sexual phase (c.f. e.g. Joosse & Veltkamp, 1970). No specimens in pre-ecdysis condition were seen.

I have, of course, considered the possibility that *D. porcellus* might only be an

ecomorph. This is not wholly inconceivable after Goto's (1972) study and also because the specimens show some integumentary structures often found in association with ecomorphosis. Moreover, if ecomorphosis were to occur in this species, it would be manifest during the summer drought, and presumably the specimens had not moulted since then. But I reject this possibility for the following reasons:

- (a) the specimens are adult;
- (b) the intestine is usually filled;
- (c) the sexes would show different types of ecomorphosis: restricted to abd<sub>5</sub> in the females, all over the body in the males;
- (d) the general morphology of the animals is very stable, anomalies virtually do not occur; only the arrangement of the spines is somewhat variable, but Isotomidae are usually not very stable in their chaetotaxy; the dental chaetotaxy is very stable;
- (e) eyes, mouth parts, and furca are very constant in shape, and do not present a reduced aspect (only the mucro is a bit short);
- (f) no "normal", "female-type" males are found in the material;
- (g) ecomorphosis due to parasitization seems excluded, since no difference could be found in either sex between heavily parasitized specimens and animals that were virtually free of Sporozoa.

Since care was taken to ensure random selection of both sexes for mounting on slides, the sex ratio  $\text{♀/♂} = 1.2$  is approximately correct.

#### ***Isotomiella minor* (Schäffer, 1896)**

Material: sample 4: 3♂ and 8 juv.; 7: 1 juv.; 29: 4 juv.

*I. minor* is, either primarily or secondarily, a cosmopolitan species. It is only surprising that the species is so rare in Crete.

#### ***Isotoma notabilis* Schäffer, 1896 (Fig. 40e)**

Material: sample 4: 1 juv.; 5: 5 juv.; 6: 2♀ and 5 juv.; 19: 1 juv.; 21: 8 juv. + 20 ex. in alcohol; 24: 18 juv.; 25: 16 juv.; 29: 1 juv.; 35: 12♀ and 10 juv.; 37: 3 juv.; 49: 1 juv.

An extremely common and widespread species.

#### ***Isotoma vaillanti* Murphy, 1958**

Material: sample 14: 8 juveniles.

Note: there can be no doubt that *I. vaillanti* is an ecomorph; but since it is impossible to guess of which species, I continue provisionally to use this name. After its description from mountainous Algeria, *I. vaillanti* was mentioned by Cassagnau (1971a) from the Greek mainland, i.e., the southern part of the Píndos range: Mt. Timfristós (Evritanía).



Fig. 40. *Dimorphotoma porcellus* n. sp. a, male genital orifice; b, antennal organ I and guarding thorn of a male specimen; c, labrum; d, antennal organ III. *Isotoma notabilis* Schäffer. e, ventral aspect of ant., *Isotoma olivacea* Tullberg s. auct. f, ventral aspect of ant,



***Isotoma olivacea* Tullberg, 1871 s. auct. (a.o. Gisin, 1960) (Fig. 40 f)**

Material (all immature): sample 23: 7; 31: 1; 41: 1.

The material is comparable to immatures of *I. "olivacea"* from western Europe. Since Dr. A. Fjellberg is preparing a revision of this group, I limit myself to giving a drawing of the antennal organ I (Fig. 40 f; juvenile specimen!).

***Isotoma viridis* Bourlet, 1839**

Material: sample 11: 2 juv.; 19: 4 juv.; 23: 1 juv.; 24: 5 juv.; 26: 3 juv.; 32: 1 juv.; 34: 1 juv.; 36: 2 juv.; 39: 1 juv.; 40: 1 ♀ and 7 juv.; 44: 1 juv.

The high proportion of immatures in *I. viridis* and *Isotomurus palustris* is striking.

***Isotomurus palustris* (Müller, 1776)**

Material: the present material comprises only immature specimens: sample 12: 1; 13: 1; 16: 1; 19: 7; 21: 8; 25: 1; 26: 1; 29: 1; 35: 9; 36: 4; 37: 1; 40: 1; 43: 1; 44: 2; 45: 1.

The larger specimens agree satisfactorily with the current interpretation of *palustris* s. str.

***Isotomurus* spec.**

*Isotoma* spec. Ellis, 1974.

Material: sample 26: 7 juv.

Discussion. The material in its unmistakable pigmentation agrees with the single (also immature) specimen that I described briefly from Rhodes. My guess that this specimen might be an ecomorph of an *Isotomurus* is corroborated by the fact that the Kriti specimens have much longer and more differentiated setae. The lasiotriches arrangement on abd<sub>2-4</sub> is, as far as I can establish 1, 3, 1. The labrum is typical for the genus; mucronal seta absent; lateral flaps of ventral tube with 3+3 setae.

**ONCOPODURIDAE*****Oncopodura crassicornis* Shoebbotham, 1911 (Fig. 41a)**

Material: sample 6: 2♂; 25: 1♀; 26: 1♀; 27: 2♀; 43: 1♀, 1♂ and 1 juv.; 44: 1 juv.; 45: 1 juv.

Note. The species has already been recorded from Rhodes (Ellis, 1974). The structure of antennal organ I underlines the affinity of the Oncopoduridae to the Isotomidae (Fig. 41 a).

## TOMOCERIDAE

**Tomocerus lamelligerus** (Börner, 1903) (Fig. 41 b-g)

Material: Sample 25: 4 specimens, including at least 1 female and 1 male (the other two may not be fully mature).

Description. Total length 2.2-3.0 mm. Pigmentation very weak, mainly on pleura of  $th_3$ , anterior margin of  $th_2$ , coxae, and frontal region of head. Scales normal, tinged dark brown.

Antennae 0.8-0.9 times body length, first two articles bearing scales. Eyes 6 on a triangular black eye patch. Labral chaetotaxy typical: 4/5, 5, 4; labral margin with 4 recurved spines. Mouth parts seemingly normal, not dissected. "Prostheca" not visible in transparency. Cephalic chaetotaxy seems unstable; anteriorly a group of about 6 setae, discally about 6+6 setae. Rear margin of head with a row of many short spines.

Trochanteral organ of  $P_3$  composed of one stiff seta on trochanter; one identical seta basally on femur (Fig. 41 e). Feet covered with scales up to the tibiotarsi. Tibiotarsal spines present, but difficult to count, because they are caducous and intergrade between strong setae.

Unguis with strong pseudonychia, and on inner lamella 4 teeth plus a slightly stronger basal tooth. Unguiculus without apical filament or outer tooth, but with a small tooth on the anterior of the two inner lamellae only (Fig. 41 b). Tenent hair strong, tubiform.

Abdomen and thorax with lasiotriches lacking accessory scales at the base. Ventral tube with many setae and scales. Retinaculum quadridentate, without scales and with only one seta on the corpus (Fig. 41 c).

Manubrium anteriorly with scales, laterally with a single row of strong setae, posteriorly with two broad longitudinal bands of many setae. Dental spines (Fig. 41 g) in two specimens 3,  $\underline{2}/4$ , 1; in the adult female 4,  $\underline{2}/$ , 1, 3,  $\underline{1}$ , and in the male 5,  $\underline{2}/$  1,  $\underline{1}$ , 3,  $\underline{1}$ . The basal spines are arranged in an irregular double row (Fig. 41 d). The spines are brown, striate, and complex. Mucro with one apical and one ante-apical tooth, and two basal teeth, the outer one having an accessory tooth. Intermediate teeth are absent. The two basal teeth each have a proximal lamella; the ante-apical tooth gives rise to a very short and low outer lamella, as well as to a conspicuously high, undulating inner lamella that stretches as far as the inner basal tooth (Fig. 41 f). Dentes basally with one pair of inner modified scales, about half as long as the accompanying normal scales.

Discussion. The species is well characterized by the combination of the presence of strongly compound dental spines and a mucro without intermediate teeth but a high lamella. The only species in the European fauna with these characters is *T. lamelligerus* (Börner, 1903), described from Calabria, and later recorded from Bulgaria (Rusek, 1965, citing an inaccessible paper by Drenowski, 1937; the material was identified by Stach) and Yugoslavia (e.g. Cvijović, 1972). A similar mucro is described in *T. terrestralis* (Stach, 1922) which has the dental spines simple, and the North American (Californian) species *T. teres* Christiansen, 1964, which differs by having the dental spines essentially simple and the tenent hair pointed or only weakly clavate.

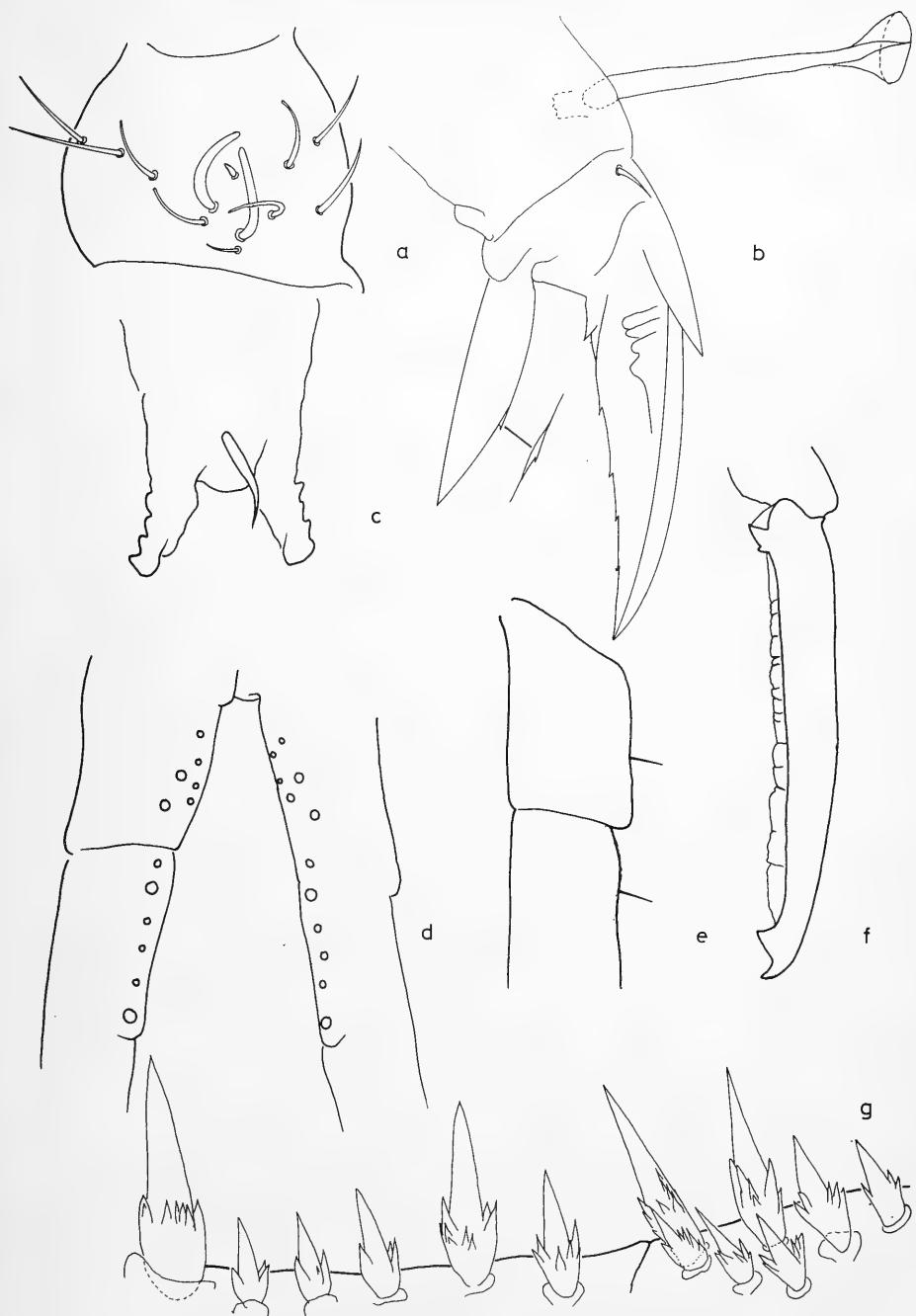


Fig. 41. *Oncopodura crassicornis* Shoenbotham. a, ventral aspect of ant., *Tomocerus lamelligerus* (Börner). b, claw of P<sub>3</sub>; c, retinaculum; d, arrangement of dental spines; e, trochanter and basal part of femur of P<sub>3</sub> with trochanteral organ; f, mucro; g, dental spines, inner view

Since Börner's description is exceedingly concise, and consequently the identification of the Greek material was not beyond doubt, I compared the Cretan specimens with a topotypical specimen, kindly loaned to me by Dr. R. Dallai, from Sienna. This specimen, an immature collected in Palmi, Calabria on 27 March, 1972, was mounted, and the chaetotaxy could not be studied. However, all other structural details agreed with the Greek specimens. The strong tooth on the inner lamella of the unguiculus mentioned by Börner is less pronounced in the specimen seen, much as in the Cretan examples.

#### CYPHODERIDAE

##### ***Cyphoderus albinus* Nicolet, 1841**

Material: 2 specimens from sample 49.

The species has a very large distributional area covering Europe.

##### ***Cyphoderus* spec. cf. *maroccanus* (Delamare, 1948) (Fig. 42 a, b)**

Material: sample 5: 1♂ and 1 presumably juvenile specimen.

The proportionally short mucro (1/7 times dens) places these specimens within the group singled out by Delamare as *Cyphoda*.

In one specimen (the male) there are 5 outer and 5 inner scales on the dens, but I am not completely certain about the number in the other specimen; in both specimens the internal apical scale is at least twice as long as the exterior one. The mucro has a vestigial subapical tooth (Fig. 42 a). The unguis has only one of the basal teeth strongly developed. An unpaired tooth is lacking in most claws, but was seen in one instance (Fig. 42 b).

The related species *C. grassei* (Cassagnau & Delamare, 1948), differs by the very narrow basal tooth on the unguis, and in having a distinct tunica.

It is very hard to allocate the two specimens: the shape of the mucro and the distributional evidence point towards identification as *grassei*, but the shape of the claw suggests *maroccanus*.

#### TROGLOPEDETIDAE

##### ***Troglopedetes cretensis* n. sp. (Fig. 42 c-e, 43 a-e)**

Material: sample 35: 1; 38: 1; 44: 2; 45: 1; 46: 3; all specimens of unknown sex, perhaps largely immature, except one ♀, the holotype, from sample 46.

Description. Total length of largest specimen, the holotype, 1.0 mm; remaining specimens 0.7-0.8 mm.

Colour white, no trace of pigment, scales in large specimens with a brown hue. Habitus paronelloid, with the conspicuous long and stiff furca.

Antennae twice head diagonal. Ant. 1: 2: 3: 4 = 3.5: 6.5: 4.8: 10.0. Ant<sub>4</sub> divided into two equal parts by a distinct suture. Ant<sub>1-2</sub> dorsally with some scales. Ant<sub>1</sub> dorsally in basal position with 4 small spines, ventrally with 2 small sensillae and 3

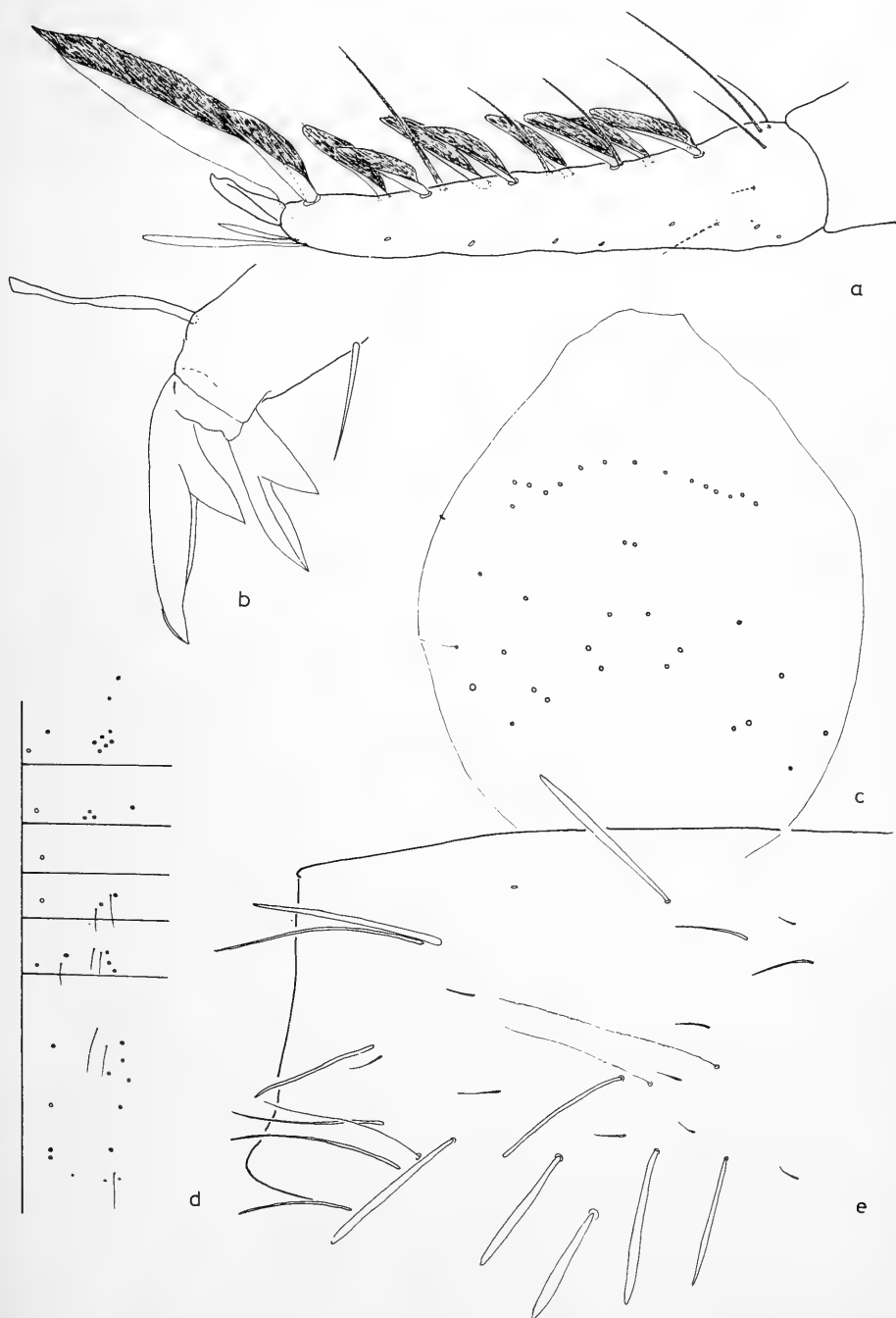


Fig. 42. *Cyphoderus* cf. *maroccanus* (Delamare). a, mucrodens; b, claw of P<sub>3</sub>. *Troglopedetes cretensis* n. sp. c, cephalic chaetotaxy; d, diagram of body chaetotaxy; e, latero-distal hair cover of abd<sub>4</sub>.

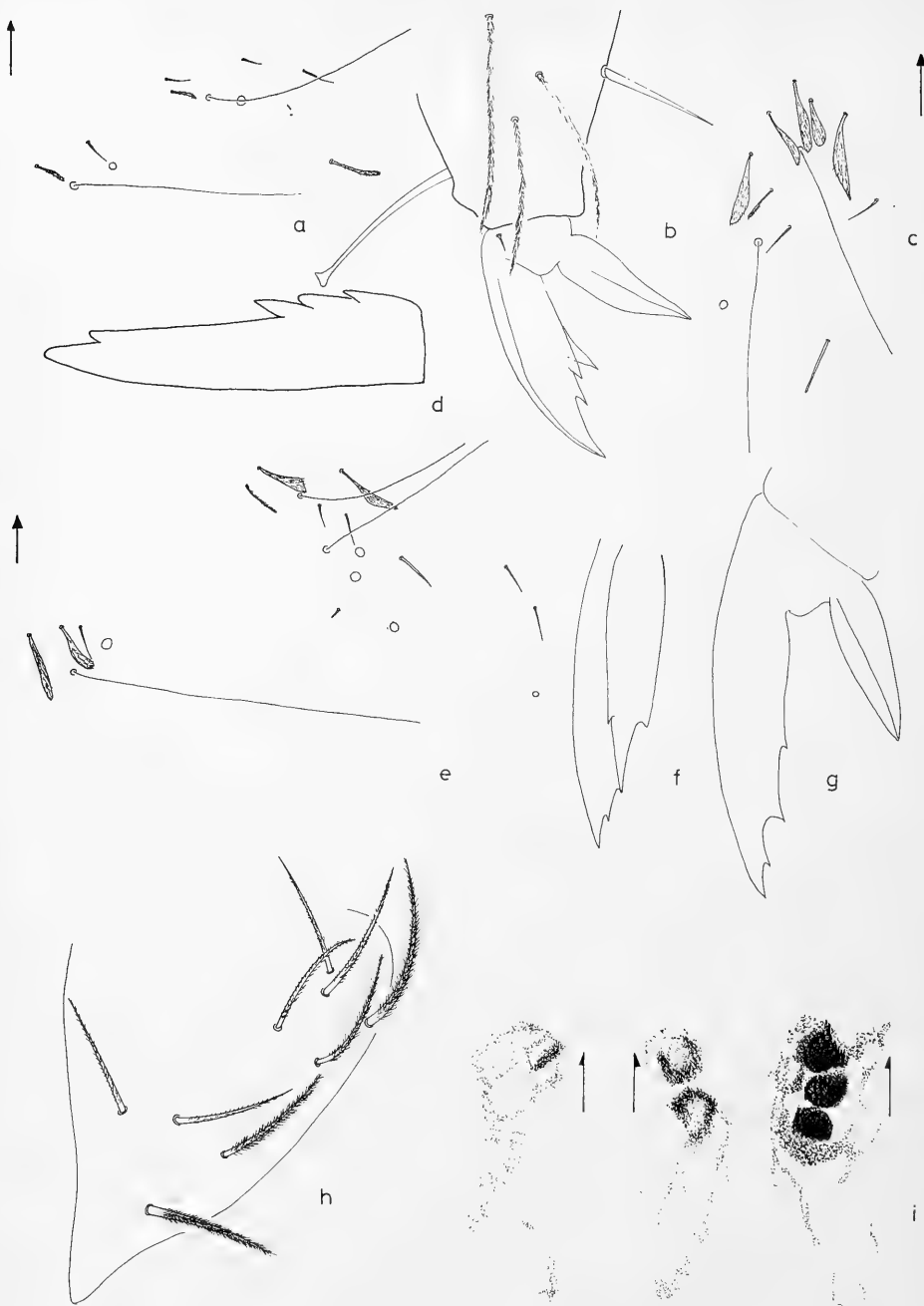


Fig. 43. *Troglopedetes cretensis* n. sp. a, lasiotriches and accompanying structures of abd<sub>2</sub>; b, claw of P<sub>3</sub>; c, lasiotriches and accompanying structures of abd<sub>4</sub>; d, mucro; e, lasiotriches and accompanying structures of abd<sub>3</sub>. *Pseudosinella paprivata* n. sp. f, inner carina of unguis; g, claw of P<sub>3</sub>; h, labial chaetotaxy; i, eye patches of three specimens at the same magnification (interference contrast microscope), to show variability in number of ocelli

sense hairs. Ant<sub>2-4</sub> with many smooth sense hairs of variable length, and with a small number of sensillae in the form of a very short spine (type F of Christiansen, 1958); sensillae of type B — short sense hairs, apically dilated and cleft — not found. No apical retractile papilla. Mouth parts normal for the family group. Labral margin with (4?) globular thickenings that I could not analyse. Prelabral setae 4/5, 5, 4. Labral chaetotaxy quite comparable to that of *Lepidocyrtus*: M<sub>1</sub>M<sub>2</sub>rEl<sub>1</sub>L<sub>2</sub>; not only r but also l<sub>1</sub> in the form of a short spine.

Ocelli absent. For cephalic chaetotaxy, see Fig. 42 c.

Feet without scales. Trochanteral organ composed of 9 smooth spines. Femora and tibiae with plumose hairs and a small number of sensillae (?) of type F referred to above. Tibiotarsus<sub>3</sub> with smooth supra-empodial hair; tenent hair distinctly clavate. Unguiculus rather broad, untoothed, unguis with well-developed basal teeth and one strong unpaired tooth (Fig. 43 b).

Ventral tube with a limited number of plumose setae at anterior and posterior faces; anterior face not easily studied, posterior with 3 + 3 type F sensillae and at least one pair of scales. Retinaculum quadridentate, corpus without scales, having only one median hair.

Manubrium: dens: mucro = 10.0: 5.8: 1.7. Manubrium anteriorly and laterally scaled, posteriorly with ciliate setae. Dens anteriorly with large scales — the distal ones as long as the mucro — posteriorly with ciliate setae and postero-internally with a row of at most 15 simple smooth spines. The spines are distally slightly longer than basally; in the middle of the dens they are half as long as width of dens. Mucro almost 5 times as long as maximally thick, with apical and subapical teeth, and postero-basally 3 or 4 sawteeth (Fig. 43 d).

Body chaetotaxy oligochaetotic (Fig. 42 d). Each segment with one pair of pseudopores. Lasiotriches: one pair on head, 2, 3, 3, on abd<sub>2-4</sub>, showing accompanying modified scales at their bases. Many microchaetae, a number of which on abd<sub>4</sub> are conspicuously long (Fig. 42 e, 43a, c, e).

To give an impression of the variability of some characters, Table 7 shows some data on the length of the specimens, the number of dental spines, and the number of dorsal teeth on the mucro.

Discussion. The new species is very close to *T. cavernicola* Delamare, 1944, described in great detail from some caves in Portugal. Differences are: the mucro is narrower in *cavernicola* with only two basal teeth (apparently constantly) and the

Table 7. Total length and numbers of dental spines and dorsal teeth of mucro in *Troglopedetes cretensis* n. sp.

Length (mm)	dental spines	mucronal teeth
1.0	15 + 15	3 + 3
0.8	12 + 12	3 + 4
0.8	? + 12	3 + 3
0.8	10 + 10	3 + 4
0.7	9 + 12	3 + 4
0.7	9 + 10	2 + 3
0.7	8 + 9	3 + 4
0.6	12 + 12	3 + 3

tenent hair in *cavernicola* is very weakly clavate. There are also differences in some chaetotactic details although in interpreting Delamare's drawing of the chaetotaxy of *cavernicola* one must include the pseudopore, which was not known at that time. The  $th_2$  of *cavernicola* are stated to show 3-4 insertions on each side within the groups of six setae; in *cretensis* this is 1 + the pseudopore. In  $th_3$  *cavernicola* has 3 + 3 insertions within the groups of 3; in *cretensis* this is 0 + the pseudopore. In  $abd_4$  *cavernicola* has 4 strong macrochaetae lateral to the anterior lasiotriches; in *cretensis* there are 5.

## ENTOMOBRYIDAE

### **Heteromurus major** (Moniez, 1889)

Material: sample 11: 1 ex.; 13: 2 ex.; 19: 1 juv.; 25: 2 ex. (1♂); 26: 3 ex. (1 juv., 1♂); 27: 4 ex. (2♀); 29: 4 ex. (1♀, 2♂); 31: 2 ex. (1♂); 35: 2 ex. (1♀ and 1 juv.); 38: 1 juv.; 43: 1 juv.

Discussion. The material is in good agreement with the specimens recorded earlier by me (1974) from Rhodes. Labial chaetotaxy is again MMREIL, and this very constantly. The smooth seta  $l_1$ , also drawn by Hühner (1970), is peculiar. These results are somewhat at variance with the information given by Martynova, Chelnokov & Rasulova (1974), who report a rather strong variability in the labial chaetotaxy of southeastern Russian *major* (MMR-IL, MMREll, MM/m . . . l, MMREll) in which  $l_2$  seems to be the only seta which is constantly smooth.

### **Heteromurus sexoculatus** Brown, 1926, bona species

Material: sample 5: 1 ex.; 6: 1 ex.

Discussion. The good luck of finding two more specimens of *H. sexoculatus* gives me the opportunity to revise my earlier opinion that *sexoculatus* is a variety of *major*, since they showed two characters which could be confirmed in the specimen from Rhodes.

The labial chaetotaxy is not completely stable, but either  $M_1m_2rel_1l_2$  or  $m_1m_2rel_1l_2$  ( $m_1$  is about  $2/3$  the length of  $m_2$ ). In one specimen this occurs asymmetrically; in another, seta  $r$  is symmetrically absent. However this may be, the number of smooth setae is much higher than in *H. major*. In conjunction with this the setae at the ventral face of the head are smooth or almost so, only becoming gradually more serrate towards the proximal and lateral regions.

The posterior face of the manubrium bears some pairs of stiff erect and virtually smooth setae, about 1.5 times the length of the normal serrate setae. The number of these hairs is difficult to establish, since they tend to fall out easily, and the number is perhaps variable; in any case, one pair is situated very proximally, and another  $3/4$  of the distance from base of manubrium; in one specimen such a seta was also observed on the dental base. Setae of this type are missing in *major*, but are present in *nitidus* and related species. No smooth setae are present on the tibiotarsi. Body chaetotaxy as in *major*.



I asked Mr. P. N. Lawrence of the British Museum whether the types of *H. sexoculatus* were still extant, and he informed me that the whereabouts of Brown's collection are unknown.

***Heteromurus nitidus* (Templeton, 1835)**

Material: sample 9: 1 juv.; 24: 1 juv.; 38: 1 ad.

The species has been recorded throughout Europe.

***Pseudosinella octopunctata* Börner, 1901**

Material: sample 4: 2 ♀ and 2 ♂; 5: 1 ex.; 6: 1 ex.; 10: 1 ♀; 11: 3 ex. (1 juv.); 12: 1 ex.; 14: 1 ♀; 20: 1 ♀; 26: 1 ex.; 29: 2 ex. (1 ♂); 30: 1 ex.; 32: 4 ex. (1 ♀); 36: 2 ex. (1 ♂); 42: 2 ex.; 45: 1 ex.; 48: 1 ex.

The species has already been recorded from Rhodes (Ellis, 1974). Recently, Da Gama (1973) recorded it from Turkey.

***Pseudosinella albida* (Stach, 1930)**

Material: sample 9: 1 ad.; 25: 2 ♀ and 1 juv.; 31: 2 ♂; 36: 1 ♂.

Discussion. The material agrees with the description given by Stomp (1971), but the pigmentation is much stronger, as is normal for Greek material (Stomp, 1972). There is a contradiction between Stomp's descriptions of 1971 and 1972 as to the presence of seta *s* on abd<sub>4</sub>. In the present material seta *s* is indeed present, as stated in the earlier publication. The species seems to be common in Greece (see also Da Gama, 1973), and is also known from Spain and Italy.

***Pseudosinella imparipunctata* Gisin, 1953**

Material: sample 4: 1 ♂; 11: 1 ♀; 14: 1 ex.; 16: 1 ex.; 21: 1 ex.; 34: 1 ♀; 35: 1 juv.; 43: 1 ♀.

Discussion. The material agrees with the literature in most currently available characters: labial chaetotaxy MrELL, chaetotaxy of abd<sub>2</sub> pABQq, seta *s* lacking on abd<sub>4</sub>, body macrochaetae R111/10/030+2, no scales on ant<sub>1</sub>. The unguis is as described by Gisin (1953), closely resembling that of *alba* (Packard, 1873).

However, the configuration of the eyes is not completely in agreement with the original description. Most of the specimens show two distinct, well-pigmented eyes, subequal and separated by slightly less than their diameter. In the two ♀ mentioned above, the eyes on one side are much closer to each other, almost touching (and again subequal). In the immature from sample 35, one side shows 3 subequal, well-spaced eyes, lying in a straight row.

*P. imparipunctata* was described from Switzerland, and has been recorded from Spain (Selga, 1973), Portugal (Da Gama, 1961), Germany (Hüther, 1961), and Bulgaria (Kosarov & Zonev, 1966).

***Pseudosinella paprivata* n. sp. (Fig. 43 f-i, 44 a, b)**

Material: sample 5: 3 ♀, 1 ♂, 2 immature ♂, 7 specimens of unknown sex, partly juv.; 9: 1 juv. (identification not definite, excluded from type-series); 27: 1 ♀, 4 juv.; 44: 2 juv. Holotype is a ♂ from sample 5.

Description. Total length 0.6 mm. Habitus normal. Scales thin. Some pigment only in and around the poorly delimited eye patch.

Antenna 1.4 times head diagonal. Ant 1:2:3:4 = 3.8:5.2:5.9:10.0. No scales on antenna.

Eye number very difficult to establish (cf. Fig. 43 i). In samples 27 and 44, 3 pigmented corneae are visible; in sample 5 (and in the doubtful specimen from sample 9) mostly 2+2, but sometimes virtually 1+2 or 1+1 ocelli can be counted. Since no other distinction could be made within the material, these differences, if real, are not considered important. Labial chaetotaxy in all specimens except 2 ♀ and 1 juv. from sample 5: M-ELL; in the three specimens mentioned: MrELL. Evidently, the reduction of seta r has led in most specimens to its total suppression. The row of setae anterior to the prelabial setae are also ciliate, though less than the prelabial ones, just as in *P. ciliata* Ellis, 1974 (Fig. 43 h).

Feet without scales. Empodium lanceolate. Tenent hair feebly clavate. Unguis with comparatively weak basal teeth, inserted rather high, and two comparatively strong distal teeth (Fig. 43 f, g).

Abd<sub>2</sub> with a rather special chaetotaxy, formulated as: --Bqq. Not only are p and a constantly absent, but also the exterior of the two microchaetae in front of the lasiotriche is absent, and at its site there is a small scale (Fig. 44 a). Abd<sub>4</sub> without seta s; seta a well ahead of e (Fig. 44 b). Arrangement of macrochaetae: R011/10/0101+2.

Mucro with subequal teeth.

Discussion. The constant absence of both a and p on abd<sub>2</sub> places this species in an isolated position among all European species described so far. It is generally agreed that *Pseudosinella* is derived polyphyletically from *Lepidocyrtus*, largely through some still extant stem species. In the present case, however, I do not know of a *Lepidocyrtus* species from which this form could have been derived.

***Lepidocyrtus lignorum* (O. Fabricius, 1775) (Fig. 44 c, d)**

Material: sample 6: 1 ex.; 20: 1 ex.; 21: 1 juv.; 23: 1; 25: 1; 30: 3 (2 juv.); 31: 3 (1 ♀); 36: 1 juv.; 37: 1 ♂; 38: 4 (2 ♀); 45: 1 juv.; 50: 3 (1 juv.).

Discussion. The specimens are in good agreement with West European material of this species, except that in some of the largest specimens the labial chaetotaxy shows some (symmetrical) duplication, resulting in the presence of an accessory seta M<sub>1</sub>' and two setae R', R'' (Fig. 44 c). But most specimens show the normal labial chaetotaxy M<sub>1</sub>M<sub>2</sub>REL<sub>1</sub>L<sub>2</sub>. Other characteristics of the species are: scales present on femora and tibiae and on ant<sub>1-3</sub>, body chaetotaxy R001/00/0101+3, chaetotaxy of abd<sub>2</sub>: paBqq, seta s lacking on abd<sub>4</sub>.



Fig. 44. *Pseudosinella paprivata* n. sp. a, chaetotaxy of abd<sub>2</sub>; b, anterior lasiotriches of abd<sub>4</sub> with associated microchaetae. *Lepidocyrtus lignorum* (O. Fabricius). c, labial chaetotaxy; d, ventral tube, anterior view. *Lepidocyrtus lignorum* forma ? e, pigmentation of abd<sub>3-4</sub>. *Lepidocyrtus serbicus* Denis. f, ventral tube, anterior view

**Lepidocyrtus lignorum** forma? (Fig. 44 e)

Material: sample 25: 2 specimens.

Discussion. The specimens agree morphologically in all details with *L. lignorum* (which occurred in the same sample). However, they show a pigmentation pattern I do not remember ever having seen in *lignorum*: two broad spots on abd<sub>3</sub>, almost filling the dorsum of that segment, leaving only a median uncoloured spot and two smaller marks postero-laterally on abd<sub>4</sub>. Also pigmented are the frontal ocellus and — weakly — the antennae. Eye patches black as usual.

It is interesting to regard this material in relation to the "*lignorum* var.?" mentioned by Da Gama (1973) from the Peloponnesus and the Ionian islands. Here, however, abd<sub>2</sub> and abd<sub>3</sub> are entirely pigmented, as well as the posterior corner of abd<sub>4</sub>. The relation between these two forms and *L. instratus* Handschin, 1924, from Switzerland and east-central Europe, merits closer study.

**Lepidocyrtus serbicus** Denis, 1936 (Fig. 44 f)

Material: sample 15: 1 ex.; 19: 1♂; 21: 1♀; 24: 2♀; 25: 13 ex. (at least 3 adults and 1♀); 27: 8 ex. (at least 2♀ and 2♂); 35: 2 ex. (1♀); 37: 1 ex.; 44: 1 ex.

Discussion. The material is in good agreement with the descriptions, but some clearly immature specimens seem to lack seta M<sub>1</sub> on the labium. Otherwise, the characters of *serbicus* are stable: body chaetotaxy R11/00/0101+2; antennae and feet without scales; labial chaetotaxy M<sub>1</sub>M<sub>2</sub>REL<sub>1</sub>L<sub>2</sub>; chaetotaxy abd<sub>2</sub>: p-B-q<sub>2</sub>; seta s lacking on abd<sub>4</sub> (and seta e rather longer than the others).

*Lepidocyrtus serbicus*, described from Yugoslavia, has been recorded from Poland (Szeptycki, 1967), and Romania (Gisin, 1965). Although some references are ambiguous, on the European mainland *serbicus* seems to be usually cavernicolous.

**Seira graeca** Ellis, 1966 (Fig. 45 a)

*Seira pillichi graeca* Ellis, 1966.

*Seira ferrarii*; Ellis, 1974.

Material: sample 38: 1♀.

The study by Dallai (1973), unfortunately received only at the end of 1974, convinced me of the importance of the chaetotactic details of th<sub>2</sub>, and forced me to re-examine my material from central Greece and Rhodes. The posterior group of macrochaetae on th<sub>2</sub> proved to consist of a tight group of 7+3+5 macrochaetae (Fig. 45 a). Only in two not fully mature specimens from Rhodes was 6+3+5 found asymmetrically.

Dallai (1973) cites two differences between *S. ferrarii* Parona, 1888, and *S. sacchii* Parisi, 1969: (1) *ferrarii* has 6+3+5, *sacchii* 7+3+5 macrochaetae posteriorly on th<sub>2</sub>, and (2) *ferrarii* has 8, as against 10 macrochaetae *sacchii* has in the transverse row between eye patch and frontal ocellus. *S. graeca* and *ferrarii* differ only in th<sub>2</sub> chaetotaxy, and thus the only remaining difference between *graeca* and *sacchii* would be the interocular macrochaetae. As a matter of fact, in

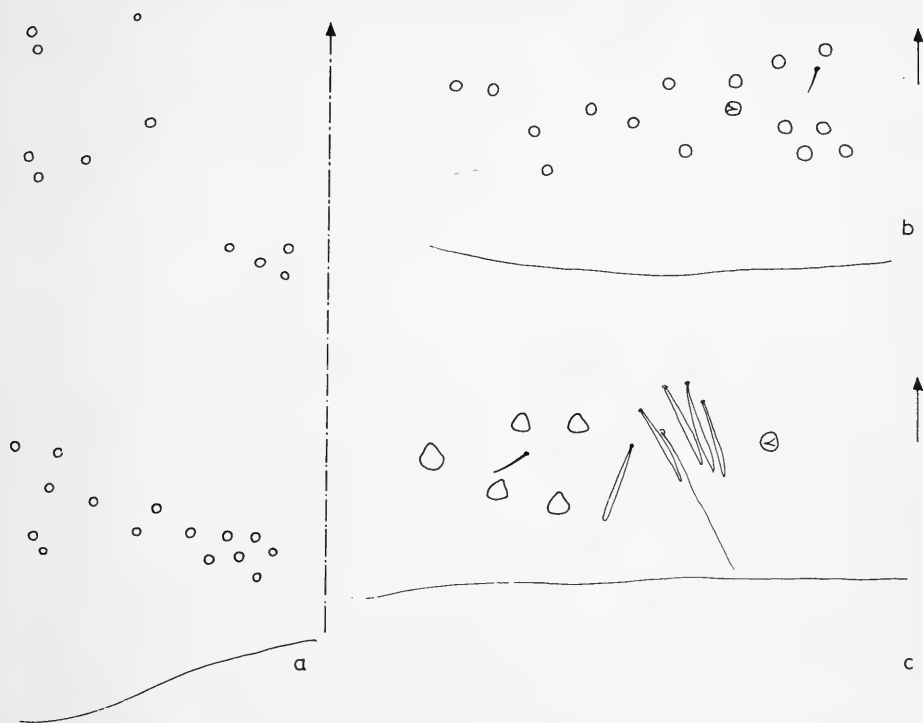


Fig. 45. *Seira graeca* Ellis. paratype. a, chaetotaxy of  $th_{1-2}$ . *Seira* spec. b, chaetotaxy of  $th_3$ ; c, dorso-medial chaetotaxy of  $abd_4$

*graeca* this number is 8+8 or, almost as frequently, 8+9. The difference between *graeca* and *sacchii* is thus very small indeed. *S. sacchii* is so far known only from Italy.

#### *Seira* spec. (Fig. 45 b, c)

Material: sample 46: 1 ♀.

The habitus of the living animal is unknown, but in chaetotactic details the specimen is very close to *S. dagamae* Dallai, 1973, except for one clear feature:  $th_3$ , which has 14 paramedian macrochaetae in *dagamae*, has 15 in the present specimen; in particular, the group postero-internally from the pseudopore has one macrochaeta more. I cannot evaluate this specimen at present (Fig. 45 b).

For convenience, I present below a practical key to the European *Seira* of which the chaetotaxy is known.

- |  |   |
|--|---|
| 1. Discal group of $th_2$ with 4 setae; anterior row on $abd_4$ simple .....                 | 2 |
| — Discal group of $th_2$ with more than 4 macrochaetae; anterior row on $abd_4$ double ..... | 7 |
| 2. Paramedian group of $abd_2$ with 5 macrochaetae .....                                     | 3 |
| — Paramedian group of $abd_2$ with 4 macrochaetae .....                                      | 5 |

3. Posterior group of  $th_2$  with 15 macrochaetae ..... 4
- Posterior group of  $th_2$  with 18-20 macrochaetae .....  
..... *domestica* Nicolet, 1841
4. Paramedian group of  $th_3$  with 14 macrochaetae .....  
..... *dagamae* Dallai, 1973
- Paramedian group of  $th_3$  with 15 macrochaetae .....  
..... unnamed species (see p. 315)
5. Posterior field of  $th_2$  with 14 macrochaetae ..... *ferrarii* Parona, 1888
- Posterior field on  $th_2$  with 15 macrochaetae ..... 6
6. Between eye patch and frontal ocellus, 8-9 macrochaetae .....  
..... *graeca* Ellis, 1966
- Between eye patch and frontal ocellus, 10 macrochaetae .....  
..... *sacchii* Parisi, 1969
7.  $th_3$  with postero-medial group (behind pseudopore) of 7-9 macrochaetae ....  
..... *lusitanica* Da Gama, 1964
- $th_3$  with postero-medial group of 4 macrochaetae .....  
..... *squamoornata* (Schtscherbakow, 1898)
- $th_3$  with postero-medial group of 3 macrochaetae ..... 8
8. Discal field of  $th_2$  with 7 macrochaetae .....  
..... *pallidipes* Reuter, 1895, sensu Loksa & Bogojević, 1970
- Discal field of  $th_2$  with 10-11 macrochaetae ..... 9
9. Anterior macrochaeta of intermediate group of  $abd_4$  twice as far from  
posterior seta in this group, as from its lateral neighbour .....  
..... *saxatilis* Gisin & Da Gama, 1962
- Three times this distance ..... *dollfusi* Carl, 1899

*S. arenaria* Da Gama, 1966, *banyulensis* Denis, 1924, *italica* (Cassagnau & Delamare, 1953) and *petrae* Jacquemart, 1973, are considered synonyms of *S. ferrarii*.

### **Entomobrya muscorum** (Nicolet, 1841)

Material: sample 8: one adult specimen.

The specimen is very pale, and the meagre pigmentation resembles most closely that of *E. pazaristei* Denis, 1936. However, the extremely long antennae of the specimen are more in favour of an identification as *muscorum*. The species has been recorded from some central European countries, Madeira, and North and South America (South, 1961).

### **Entomobrya handschini** Stach, 1922

Material: sample 15: 3 ♀, 7 adults of unknown sex and 1 juv.; 22: 1 ♀, 3 adults of unknown sex and 1 juv.; 26: 1 juv.; 27: 1 juv.; 38: 4 ♀ and 2 ♂.

This characteristic species, one of the few truly epigeic species encountered in Crete, was described from Hungary, and has since been recorded from many countries in south-eastern Europe and from Spain.

**Entomobrya multifasciata** (Tullberg, 1871)

Material: sample 15: 3 adults; 22: 7 ♀, 2 ♂, and 1 juv. + 7 ex. in alcohol; 27: 1 juv.; 38: 1 ♀, 1 ♂, 1 juv., and 3 adults of unknown sex, + 7 ex. in alcohol.

This common European species has already been recorded from Rhodes.

**Entomobrya cf. multifasciata** (Tullberg, 1871)

Material: sample 23: 1 ♀, 1 ♂ and 2 specimens of unknown sex; 32: 1 ex.; 33: 1 ♂ and 3 juv.; 42: 1 ♂ and 2 juv.; 49: 2 ex. (1 juv.).

All these specimens are wholly or almost entirely depigmented; the few traces of pigment and the few reliable morphological characters do not contradict identification as *multifasciata*.

## NEELIDAE

**Megalothorax incertus** Börner, 1903

Material: sample 23: 1 ex.; 25: 2 ex.; 27: 1 ex.; 35: 1 ex.; 36: 2 ex.; 43: 2 ex.; 44: 3 ex.; 45: 2 ex.

The species has already been recorded from Rhodes. I am not completely convinced as to the identification of the specimen from sample 23.

## SMINTHURIDAE

**Sminthurides malmgreni** (Tullberg, 1876)

Material: sample 26: 1 ♀, 3 ♂, and 5 juv.

The species has been recorded from most European countries, North America, and Japan; records from the southern Palaearctis include Portugal, Spain, Yugoslavia, Romania, N. Africa, and the Azores.

**Sphaeridia pumilis** (Krausbauer, 1898) sensu Massoud & Delamare  
Deboutteville, 1964

Material: sample 6: 1 ♀; 7: 2 ♀ and 1 ♂; 10: 4 juv.; 17: 1 ♂; 18: 5 ♀, 3 ♂, and 9 juv.; 19: 1 ♀; 21: 1 ♂ and 2 juv.; 23: 6 ♀ and 2 ♂, and about 120 ex. in alcohol; 24: 1 ♀ and 2 ♂; 25: 3 ♀; 26: 3 ♀; 27: 2 ♀ and 2 ♂; 29: 1 ♀; 32: 10 ex. in alcohol; 33: 7 ♀ and 3 ♂; 34: 2 ♀; 35: 2 ♀; 36: 4 ♀ and 1 ♂; 37: 1 ♀; 41: 1 ♂; 42: 2 ♀; 43: 1 ♀; 45: 1 ♂; 49: 1 juv.

This common and widespread species has already been recorded from Rhodes.

## SMINTHURIDAE

**Arrhopalites spec.**

Material: sample 4: 1 juv.; 25: 2 juv.; 43: 1 juv.; 44: 4 juv.

The material is too young to permit speculation about the species identification.

**Sminthurinus aureus** (Lubbock, 1862)

Material: sample 4: 3 juv.; 6: 1 ♀; 7: 2 ♂; 23: 3 juv.; 24: 1 juv.; 36: 5 juv.; 41: 5 ♀, 3 ♂, and 4 juv.; 43: 1 ♀.

Discussion. The identification of isolated immatures (samples 4, 23, 24, and 36) can of course only be conjectural. The species is widespread throughout Europe. None of the specimens shows the "typical" yellow coloration; all are marked with blue, usually well-delimited patches, which in some instances cover the major part of the body. The general habitus is rather similar to that of *S. reticulatus* Cassagnau, 1964, from the Pyrenees.

**Sminthurinus spec. aureus group**

Material: 3 immatures from sample 18.

**Sminthurinus alpinus bisetosus** n. ssp. (Fig. 46 a, b)

*S. spec.* near *alpinus* Gisin, 1953; Ellis, 1974.

Material: sample no. 970.010 from Rhodes, Línos, 1 ♂ and 1 juv.; from Kríti, sample 19: 2 juv.; 21: 1 ♂; 23: 4 juv.; 24: 1 juv.; 27: 6 juv.; 31: 1 ♂; 43: 1 ♂; 44: 1 ♀. Holotype: the female from sample 44.

In the discussion on the two specimens from Rhodes, I noted as divergent from *S. alpinus* Gisin, 1953, the two (instead of one) setae on the corpus tenaculi and the number of setae in the eye patch ("two, as seen in profile" — instead of one). Now that I have more material, the latter observation seems rather dubious. Young specimens, with the eye spot slightly transparent, seem to have only one seta in the eye patch. This character, interesting though it may be, is of limited practical use. The number of setae on the retinaculum is in all adults definitely two; doubt exists in some immatures, where the two setae differ developmentally. The wart on ant<sub>3</sub> is in the Greek material weakly trilobed, but this can also occur in material of typical *alpinus* (Fig. 46 b). In all other characters, notably the distinct dental chaetotaxy, the Greek material resembles *alpinus*, and I consider it most appropriate to evaluate the single difference in the retinaculum as a subspecific one.

After its description from Switzerland and Austria, *alpinus* was recorded from the Tatra (Nosek, 1969), Bulgaria (Rusek, 1965), and India (Choudhuri & Roy, 1972). The record from India needs confirmation.

**Stenognathellus cassagnai** Yosii, 1966 (Fig. 46 c)

*S. denisi* Cassagnau, 1953; Ellis, 1974.

Material: sample 27: 1 ♀; 36: 1 juv.; 45: 2 ♂.

Discussion. Dr. J.-M. Betsch, upon inspecting my only female from Rhodes, drew my attention to some distinctions with respect to true *denisi*: the middorsal seta on abd<sub>6</sub>, which is deeply bifurcated in *denisi*, is simple in *cassagnai*. More-



over the dens has two latero-distal setae (anterior to the distal whorl) in *denisi*, but only one in *cassagnai* (Fig. 46 c).

The Greek material is in good agreement with the species of Yosii, described from Nepal, except that the eye patch is well pigmented in the Greek material, and ant<sub>3</sub> is perhaps slightly less inflated. The appearance of this inflation depends strongly however, on the observation angle. Until now, the species had not been found again since its description.

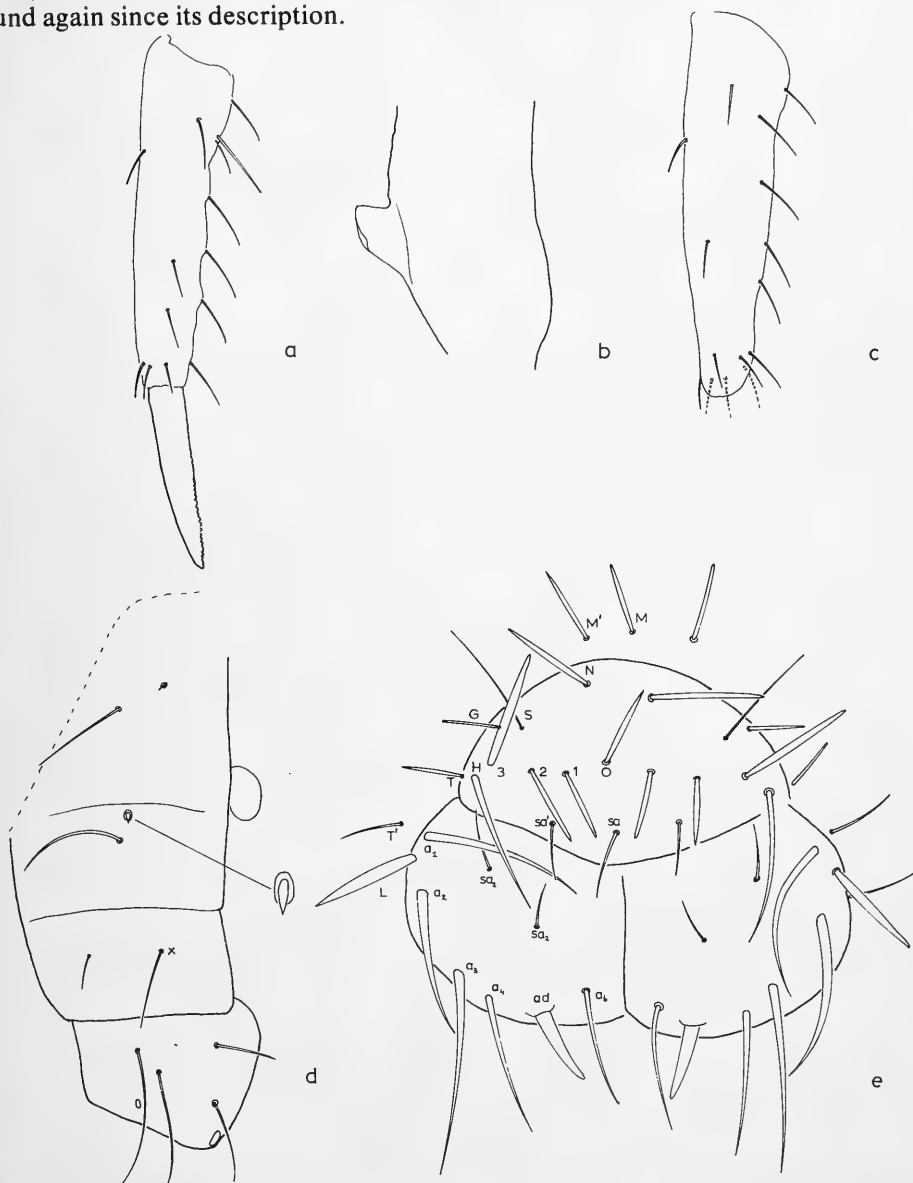


Fig. 46. *Sminthurinus alpinus bisetosus* n. ssp. a, mucrodens; b, wart on ant., *Stenognathellus cassagnai* Yosii. c, dens. *Sminthurus nigromaculatus* Tullberg. d, subcoxae 1 and 2 and coxa of P<sub>3</sub>; the seta marked x on subcoxa 2 is absent in *S. viridis*. *Ptenothrix italica* Dallai. e, female postabdomen

***Sminthurus multipunctatus* Schäffer, 1896**

Material: sample 15: 1 ♀.

This species has been recorded from southern and eastern Europe.

***Sminthurus flaviceps* Tullberg, 1871**

Material: sample 27: 1 juv.; 35: 1 juv.; 38: 3 juv.

This species, described from Sweden, has been recorded from Germany and most southern and eastern European countries. The record from the Netherlands (Buitendijk, 1941) is erroneous, as I was able to verify through examination of the original material.

***Sminthurus nigromaculatus* Tullberg, 1871 (Fig. 46 d)**

Material: sample 15: 23 juv.; 21: 1 juv. (cf.); 26: 1 juv. (cf.); 35: 1 ♀; 36: 1 ♂ and 3 juv.; 38: 6 juv. + 23 specimens, presumably also immature, in alcohol; 46: 1 ♂.

Discussion. Many authors have been reluctant to accept *nigromaculatus* as a good species, because of the minimal set of characters available to distinguish it from *viridis* (Linnaeus, 1758): a preference for drier habitats, for pollen as food (little or no plant epidermis is consumed), and the presence of two (sometimes one) dark spots on the postabdomen. I think that I have now found a good morphological character. Subcoxa 2 of  $P_3$  in *viridis* has one rather thin hair; *nigromaculatus* has the same, but also anteriorly another stouter hair (Fig. 46 d). The latter is found in *nigromaculatus* in the Netherlands and Rhodes (my separation of *viridis* and *nigromaculatus* in material from Rhodes is thus corroborated) and in the present *nigromaculatus* from Crete. The character holds for larger immatures, but very young immatures of *nigromaculatus*, which usually already have the spots on the postabdomen, show only the single hair of *viridis* — but in such specimens the number of setae on the coxa of  $P_3$  is 2, instead of 4, and the setae on the dens are fewer in number.

Comparison of the situation in *S. nigromaculatus* with that in other Symphypleona (*Allacma*, *Neosminthurus*, *Lipothrix* of the same subfamily, *Bourletiella* and *Deuterosminthurus* of the Bourletiellinae, and even *Dicyrtoma* of the Dicyrtomidae) shows that in the others subcoxa 2 of  $P_3$  has only one seta, which, to judge from its appearance and location, is homologous with the single seta in *S. viridis*. I therefore consider the possession of an extra seta by *S. nigromaculatus* to be an apomorphous character. It is a bit surprising, however, that this character is also present in *Caprainea echinata* (Stach, 1930) and *C. marginata* (Schött, 1893).

Within the genus *Sminthurus* s. str., I found that *S. guthriei* Stach, 1920, shows the plesiomorphous state, but *S. multipunctatus* Schäffer, 1896, and *S. maculatus* Tömösvary, two species which are very close to *nigromaculatus*, possess the apomorphous character state.

The stability of the chaetotaxy in the coxal region of  $P_3$  is great. Both *viridis* and *nigromaculatus* are very common in the Dutch fauna and generally in Europe.

Among the large material available I found only one aberrant specimen, an adult ♀ of *nigromaculatus* from the Netherlands in which the extra seta was absent on one side.

The specimens from Crete are all intensely mottled with blue pigment all over the body. This also applies to the immatures, which excludes the possibility of a gradual darkening of adult specimens by subcutaneous accumulation of waste products. In general appearance they have no resemblance to the *nigromaculatus* from Rhodes.

It thus seems that *viridis* and *nigromaculatus* are two well-separated species which must have evolved in a comparatively remote past. *S. viridis*, the most primitive of the two, has not evolved any further and remained monomorphous. *S. nigromaculatus*, on the contrary, is in a state of evolutionary radiation and the species comprises a number of forms, many of which doubtless have not yet reached the level of species.

Only the refined methods of beta-taxonomical approach can clarify this complex. Its recognizable members are "*maculatus*", the pale, two-spotted western European *nigromaculatus*, the dark marbled *nigromaculatus* from southern Europe, and the single-spotted *nigromaculatus* described from Rhodes.

#### ***Caprainea echinata* (Stach, 1930)**

Material: sample 19: 1 juv.; 25: 4 juv.; 29: 4 juv.; 31: 1 ♀ and 1 juv.; 44: 3 juv.

This Mediterranean species has already been mentioned from Rhodes.

#### ***Neosminthurus natalicus* Ellis, 1974**

Material: sample 24: 2 juv.; 25: 2 juv.; 35: 1 ♂ and 4 juv.; 44: 4 juv.

This apparently Mediterranean species was previously known from Ibiza and Rhodes.

### **DICYRTOMIDAE**

#### ***Dicyrtoma* (*Dicyrtoma*) *melitensis* Stach, 1957**

Material: sample 46: 1 immature specimen.

Discussion. The identification is made with some reservation, because the ungicular filament of P<sub>1</sub> of both feet is distinctly knobbed. The dental chaetotaxy, however, points to *melitensis*. The species has been described from Malta and was recorded from Stromboli (Altner, 1961), Sardinia (Parisi, 1969), and the small Italian island of Pianosa (Dallai, 1969b).

#### ***Dicyrtomina* (*Calvatomina*) cf. *articulata* Ellis, 1974**

Material: sample 27: 6 juv.

The material unequivocally belongs to the subgenus *Calvatomina* Yosii, 1966, but is too young to be attributed with certainty to *articulata*.

***Ptenothrix italica* Dallai, 1973 (Fig. 46 e)**

Material: sample 31: 1 ♀.

The single specimen is in good agreement with Dallai's description of *italica*, from southern Italy. Since Dallai did not have females, I add a drawing of the female postabdomen. The anal appendages are comparatively thick (Fig. 46 e). Although *Ptenothrix cavicola* Cassagnau & Delamare Deboutteville, 1955, described from the Lebanon, is very close to *italica*, on the basis of the few distinctive characters available (pigmentation of ant<sub>2</sub>, presence of two instead of three teeth on lateral carina of unguis) the Cretan specimen is to be attributed to the western species.

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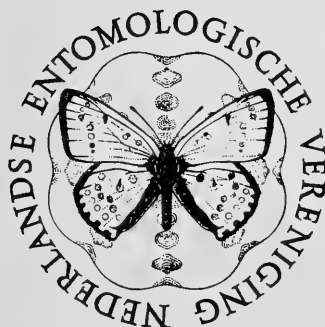
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

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DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

WARREN T. ATYEO & PAUL C. PETERSON. — The feather mite genera *Zumptia* Gaud. & Mouchet and *Parazumptia* gen. nov. (Acarina, Analgoidea), p. 327—335, fig. 1—14.



# THE FEATHER MITE GENERA *ZUMPTIA* GAUD & MOUCHET AND *PARAZUMPTIA* GEN. NOV. (ACARINA, ANALGOIDEA)<sup>1)</sup>

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With 14 figures

## ABSTRACT

*Parazumptia gallinulae* gen. nov., spec. nov., is described from *Gallinula chloropus* (Rallidae), Luzon, Philippine Islands, and India; the genus *Zumptia* Gaud & Mouchet, 1959, is redefined; *Z. dermoglyphoides* Gaud & Mouchet, 1959, is illustrated, and *Z. macclurei* spec. nov. is described from *G. chloropus*, Luzon.

The feather mite fauna of the avian family Rallidae is varied. Each genus of Analginae (Analgidae) and Pterolichidae associated with these birds contains many species. Conversely, mites assigned to the subfamily Xolalginae (Analgidae) are highly modified and each named species has been the basis of a monobasic genus. Some of these xolalgine species have a wide host range, others are known from single collections or from single localities. Extremes of these associations are exemplified by *Gymnalloptes pallens* (Trouessart & Neumann, 1888), known to occur on eight species of Rallidae from Eurasia, Africa, and the Philippine Islands, and by *Zumptia dermoglyphoides* Gaud & Mouchet, 1959, known only from the type series.

In the present paper three taxa will be described, a new monobasic genus and second species of *Zumptia*, all discovered in collections made by members of the Migratory Animal Pathological Survey in Southeast Asia. Including the new taxa, there are eight species assigned to seven genera of Xolalginae from the Rallidae; the host-parasite associations, either previously recorded (Atyeo, 1974; Gaud, 1968, 1974) or new are:

*Fulica atra* (L., 1758), european coot

*Analloptes megnini* Trouessart, 1885: Morocco

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): Morocco, India

*Gallinula chloropus* (L., 1758), common gallinule, moorhen

<sup>1)</sup> Research supported by the National Science Foundation (BMS75-03394) and the Research Council, Youngstown State University.

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): France, Madagascar  
*Parazumptia gallinulae* gen. nov., spec. nov.: Philippine Islands, India (new records)

*Zumptia macclurei* spec. nov.: Philippine Islands (new record)

*Limnecorax flavirostris* (Swainson, 1837), black crane

*Beaucourneuella loculosa* Gaud, 1974: Africa (1 ♀)

*Cryptosikya protalgoides* Gaud, 1971: Cameroons

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): Cameroons

*Zumptia dermoglyphoides* Gaud & Mouchet, 1959: Cameroons

*Podica senegalensis* (Vieillot, 1817)

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): Cameroons

*Porzana parva* (Scopoli, 1769), little crane

*Dogielacarus uncitibia* Dubinin, 1949: France, U.S.S.R.

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): Europe, Morocco, Iran (new record)

*Porzana fusca* (L., 1766), ruddy crane

*Analloptes megnini* Trouessart, 1885: Philippine Islands (new record)

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): Philippine Islands (new record)

*Rallus aquaticus* (L., 1758), water rail

*Analloptes megnini* Trouessart, 1885: Europe

*Beaucourneuella loculosa* Gaud, 1974: France

*Gymnalloptes pallens* (Trouessart & Neumann, 1888): France

Five of the above feather mites, *Dogielacarus uncitibia*, *Cryptosikya protalgoides*, the two species of *Zumptia*, and *Parazumptia gallinulae* can be considered having special modifications. Based on collections from over half of the species of Rallidae, these mites have extremely limited host distributions, occur sporadically, have a low rate of infestation, and probably maintain low populations on individual birds. It could be concluded that each of these five mite species have a limited and specific microhabitat and that each must encounter considerable pressure when becoming established on a new host individual.

In the descriptions below, the terminology for chaetotaxal signatures follows Atyeo & Gaud (1966). Type materials are deposited in the University of Georgia (UGA), the British Museum (Natural History) (BMNH), the National Museum of Natural History (NMNH), and the collection of J. Gaud (GAUD).

## Family ANALGIDAE

### Subfamily XOLALGINAE

#### *Zumptia* Gaud & Mouchet

*Zumptia* Gaud & Mouchet, 1959: 526; Gaud, 1968: 25; Atyeo, 1974: 479. Type species: *Zumptia dermoglyphoides* Gaud & Mouchet, 1959.

Diagnosis. Xolalgine mites lacking setae *sR* on trochanters I, II; humeral setae short, basally dilated, apically attenuated; subhumeral setae ventral to humerals, short, setiform; dorsal shields reduced; long, narrow metapodosomal shields lateral to hysterosomal shield; dorsal hysterosomal gland well developed (?); hysterosomal setae *dI* absent, *II* positioned posterolateral on propodosoma; epimerites I Y-shaped; legs with four functional segments (femora and genua fused); tarsi I, II with whorl of four setae near midlength (*la*, *ra*, *wa*, *aa*). Males with dentate adanal discs; well-defined posterior lobes with at least interlobar membrane well developed; genital organ small, reflexed; genital region surrounded by circular striae; ventral setae with one pair lateral and one pair immediately posterior to genital region; genital discs anterolateral to genital organ; legs III equal to or greater than legs IV. Females with characteristic epigynium, i.e., anterior margin straight, posterior margin concave.

The two species of *Zumptia* are known from limited materials, *Z. dermoglyphoides* from the original series of five specimens and *Z. macclurei* spec. nov. from three collections from the Philippine Islands and India. The poor condition of the two specimens of *Z. dermoglyphoides* available for study precludes a complete redefinition of the genus as certain structures are not visible, e.g., dorsal hysterosomal glands which are not apparent but are probably present.

The interpretation of the tarsal chaetotaxy for *Zumptia* and *Parazumptia* indicates the presence of setae normally found in the Acaridae but not present in the Analgoidea, that is, setae *aa* on tarsi I and II. In the Analgoidea four ventral and ventrolateral setae occur, they are *la*, *ra*, *wa*, and *s*; in these instances, *s* is near the apex on the midventral surface and occurs on legs I-IV. In the taxa under consideration, the fourth seta is not considered to be seta *s* as it occurs only on legs I and II and all setae occur in a whorl. Another explanation for this seta would be that it is *ba*, but *ba* in known Analgoidea occurs on the dorsal surface either in close proximity to  $\omega 1$  or in the interspace between  $\omega 1$  and  $\omega 3$ .

Striation patterns have not been noticeably different in the analgoid taxa, but between the species of *Zumptia* and *Parazumptia*, there are striking differences. On the dorsal propodosoma in the area between the posterior margin of the propodosomal shield and the sejugal suture and including the scapular setae, *Zumptia* species have the striae forming a pattern of inverted V's and U's; in *Parazumptia*, the propodosomal striae are horizontally directed and parallel. On the propodosomal venter, *Zumptia* species have the striation pattern as a series of V's with the posterior terminations of the more lateral striae bent toward the meson; in *Parazumptia*, the striae are parallel and the posterior terminations are bent laterad or are continuous with hysterosomal striae.

The last major difference between the two genera relates to the pretarsal structures (compare Fig. 6 and 11). The divided central plate of *Zumptia* is characteristic of numerous xolalgine genera; the modifications of the *Parazumptia* pretarsus are found in *Cryptosikya* and *Dogielacarus* (Atyeo, 1974).

### ***Zumptia dermoglyphoides* Gaud & Mouchet (Fig. 1—4)**

*Zumptia dermoglyphoides* Gaud & Mouchet, 1959: 526—7, Fig. 12A, B; Gaud, 1968: 26.

The species is known only from the type series consisting of two males, two females, and one nymph. The type host, *Limnecorax flavirostris*, has been repeatedly examined by Gaud and others, but to date, there has never been any reported success in recollecting *Z. dermoglyphoides*. Gaud (1968) discusses the possibility that the *L. flavirostris* specimens might have been misidentified, but he

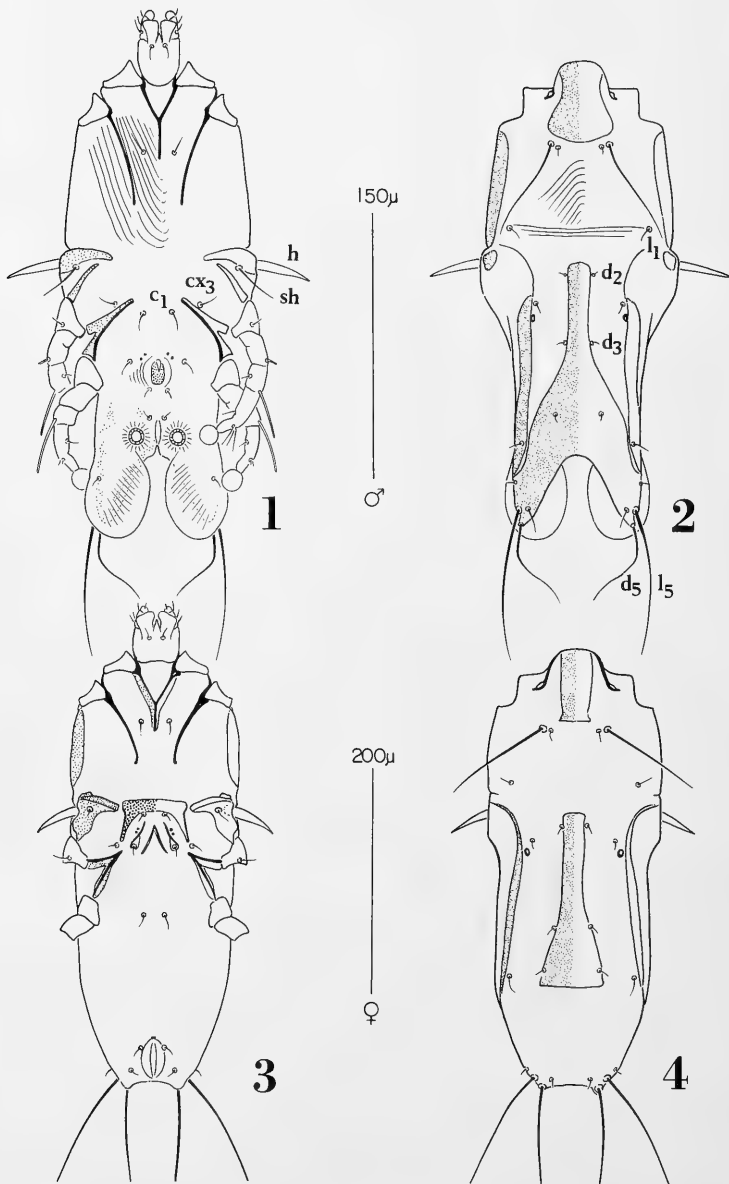


Fig. 1-4. *Zumptia dermoglyphoides* Gaud & Mouchet: ventral (1) and dorsal (2) aspects of male; ventral (3) and dorsal (4) aspects of female. Setae: *c1*, central; *cx3*, coxal; *d 2-5*, *l1-5*, dorsal and lateral hysterosomals; *h*, humeral; *sh*, subhumeral



suggests that this is probably not the case as the other mites in the collection are known ectoparasites of this bird species.

The species will not be formally redescribed as the study specimens are in poor condition — our illustrations are in reality probable reconstructions as relates to the hysterosomal shields.

Type data. From *Limnocorax flavirostris* (Swainson, 1837) (Rallidae): ♂ holotype, 1 ♂, 2 ♀ paratypes, Yaoundé, Cameroons, April, 1958, J. Mouchet. The type series is in the collection of J. Gaud.

### ***Zumptia macclurei* spec. nov. (Fig. 5-9)**

The males of *Zumptia dermoglyphoides* and *Z. macclurei* are easily separated; in the former species, legs III and IV are subequal and in *Z. macclurei*, legs III are much larger than legs IV.

Male (holotype). Length, including gnathosoma and terminal lobes 270  $\mu$ , width 108  $\mu$ . Idiosoma broad, gently tapering posterior to humeral setae to deeply cleft terminus. Dorsal propodosoma with shield small, not extending to scapular; area between posterior margin of shield and sejugal suture with inverted V and U striations. Dorsal hysterosoma with setae *d2-d4* internal to shield margins; terminus with deep U-shaped cleft 37  $\mu$  in height; membrane extending posterior to setae *l5*. Ventral idiosoma with epimerites I Y-shaped, with surface fields; striae obliquely directed and meeting at meson in V-configurations posterior to epimerites I; humeral setae dagger-shaped, 46  $\mu$  in length; subhumeral ventral to humerals and setiform; setae *c3* each on small plate posterior to genital organ; adanal discs dentate with striae radiating from corolla. Legs 4-segmented (genua and femora fused); setae absent on trochanters I, II; tarsi I, II with whorl of 4 setae near midlength; setae *s* absent; tarsus IV with setae *d, e* as short spines inserted on apicodorsal protuberance.

Female (paratype). Length, including gnathosoma 393  $\mu$ , width 139  $\mu$ . Idiosoma elongate, parallel-sided, posteriorly truncated. Propodosoma with striae directed dorsally and ventrally as in male. Hysterosoma with narrow, posteriorly truncated shield bearing setae *d2 - d4* at margins, ventral hysterosoma and legs as figured.

Type data. From *Gallinula chloropus* (L., 1758) (Rallidae): ♂ holotype, 12 ♂, 19 ♀ paratypes, Dalton Pass, North Vizeaya, Luzon, Philippine Islands, February 18, 1967, U.S. Migratory Animal Pathological Survey team (NU 13,442). Holotype and paratypes: UGA; paratypes: AMNH, BMNH, NMNH, GAUD.

Remarks. The new species is named for Dr. H. Elliott McClure, recently retired from the Migratory Animal Pathological Survey, who over the course of many years has sent us thousands of feather mite collections from Southeast Asia.

### ***Parazumptia* gen. nov.**

Diagnosis. Xolalgine mites lacking setae *sR* on trochanters I, II; humeral setae long, setiform; subhumeral setae anteroventral to humerals, setiform; propodosomal shield reduced; hysterosomal shield rather large; long, narrow metapodosomal shields lateral to hysterosomal shield; dorsal hysterosomal gland well

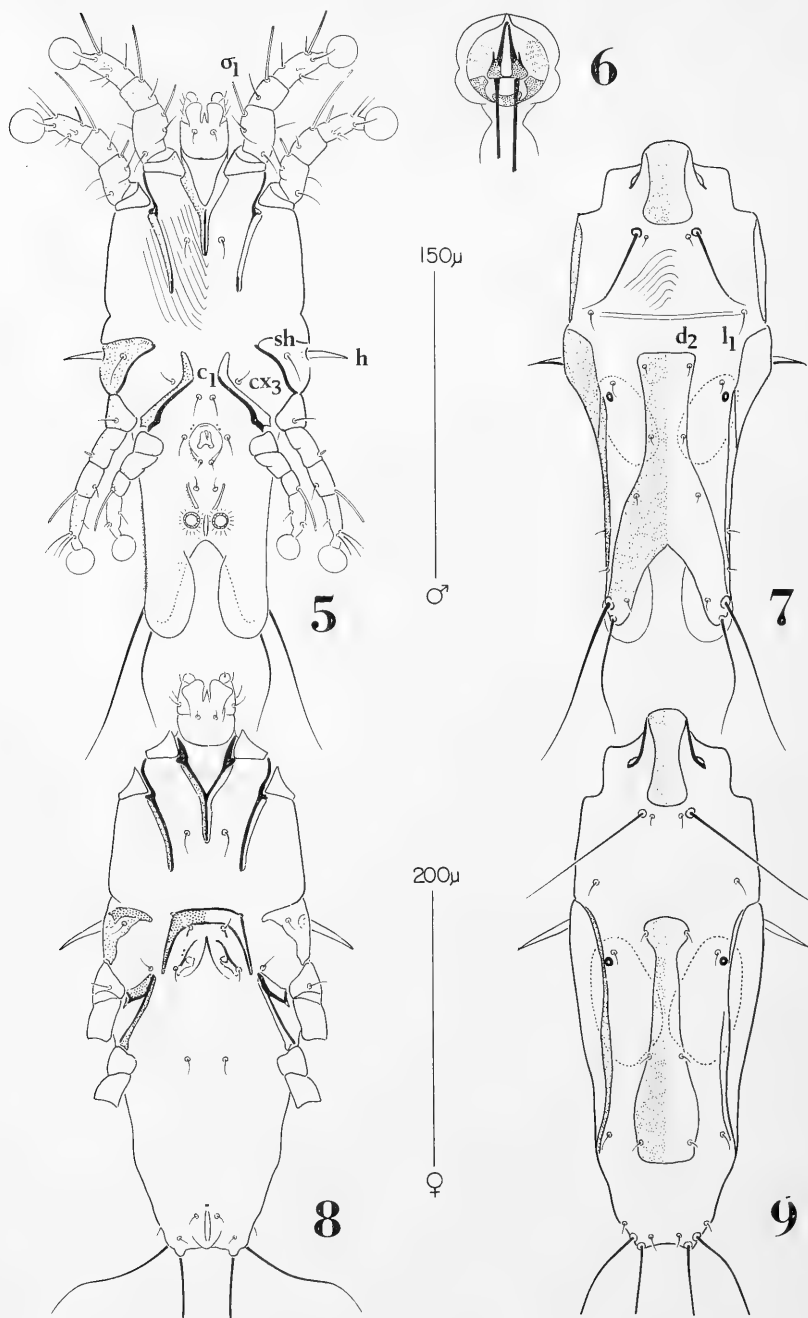


Fig. 5-9. *Zumptia macclurei* spec. nov.: ventral (5) and dorsal (7) aspects of male; enlarged pretarsus (6); ventral (8) and dorsal (9) aspects of female. Setae:  $cl$ , central;  $cx3$ , coxal;  $h$ , humeral;  $d_2$ ,  $l_1$ , dorsal and lateral hysterosomals;  $sh$ , subhumeral

developed; two pairs of hysterosomal setae absent (*d1*, *d2*), *II* positioned posterolateral on propodosoma; epimerites I Y-shaped; legs with four functional segments (femora and genua fused); tarsi I, II with whorl of four setae near midlength. Males with dentate adanal discs; well-defined posterior lobes with extra- and interlobar membranes, latter incised at midlength; genital organ small, reflexed; genital region partially surrounded by well-defined pregenital apodeme in which genital discs are incorporated; ventral setae as figured, with one pair obviously associated with coxae IV (*cx4*); legs III, IV subequal in length, legs IV slightly larger than III in diameter. Female similar to male in basic characteristics; epigynum small, transverse, and not extending to level of genital discs.

Type species: *Parazumptia gallinulae* spec. nov.

***Parazumptia gallinulae* spec. nov. (Fig. 10-14)**

This taxon is superficially similar to species of *Zumptia* in that the dorsal shields are weakly developed, the legs are four-segmented, and the males have deeply cleft idiosomata with each lobe bearing at least one large interlobar membrane. *Parazumptia gallinulae* is easily distinguishable from the known species of *Zumptia* by the long, setiform humeral setae; the same setae in *Zumptia* are short and dagger-shaped.

Male (holotype). Length, including gnathosoma and terminal lobes 340  $\mu$ , width 154  $\mu$ . Idiosoma broad, gently tapering behind humeral setae to deeply cleft terminus. Dorsal propodosoma with shield small, granulated, not extending to scapular setae; area posterior to shield, including insertions of scapular setae with transverse striae with superimposed sclerotization. Dorsal hysterosoma with weakly developed shield; two pairs of setae absent [*d1* and *d2* (?)]; narrow sclerotized band lateral to dorsal gland opening; hysterosomal glands large; terminus with deep V-shaped cleft 93  $\mu$  in height; each lobe bearing membranes on inner and outer margins. Ventral idiosoma with epimerites I Y-shaped, with stem extending almost to sejugal region; striae vertically directed between epimerites I, II and between epimerites II and ventral margin of scapular shield; subhumeral setae fine, anteroventral to humeral setae; setae *c1* and *cx3* in transverse line; setae *c2* and *a* within apodemes connecting pregenital apodeme and terminus; setae *c3* (*cx4*) near trochanter IV; genital discs incorporated in pregenital apodeme; adanal discs dentate with prominent rays radiating from corolla. Legs four-segmented (genua and femora fused); setae *sR* on trochanters I, II absent; tarsi I, II with whorl of 4 setae near midlength (*ra*, *la*, *wa*, *aa*); setae *s* absent; tarsus IV with setae *d*, *e* as short spines inserted on apicodorsal protuberance.

Female (paratype). Length, including gnathosoma 385  $\mu$ , width 150  $\mu$ . Idiosoma with small, weakly developed shields, terminus truncated. Dorsal propodosoma with shield as in male, but area posterior to shield with striae as in other regions, i.e., without superimposed sclerotization; other aspects except setal positions similar to male. Ventral idiosoma with epimerites I, II similar to male; epigynum small, not extending to genital discs; other features as figured.

Type data. From *Gallinula chloropus* (L., 1758) (Rallidae): ♂ holotype, 9 ♂, 7 ♀, Dalton Pass, North Vizeaya, Luzon, Philippine Islands, February 18, 1967, U.S.

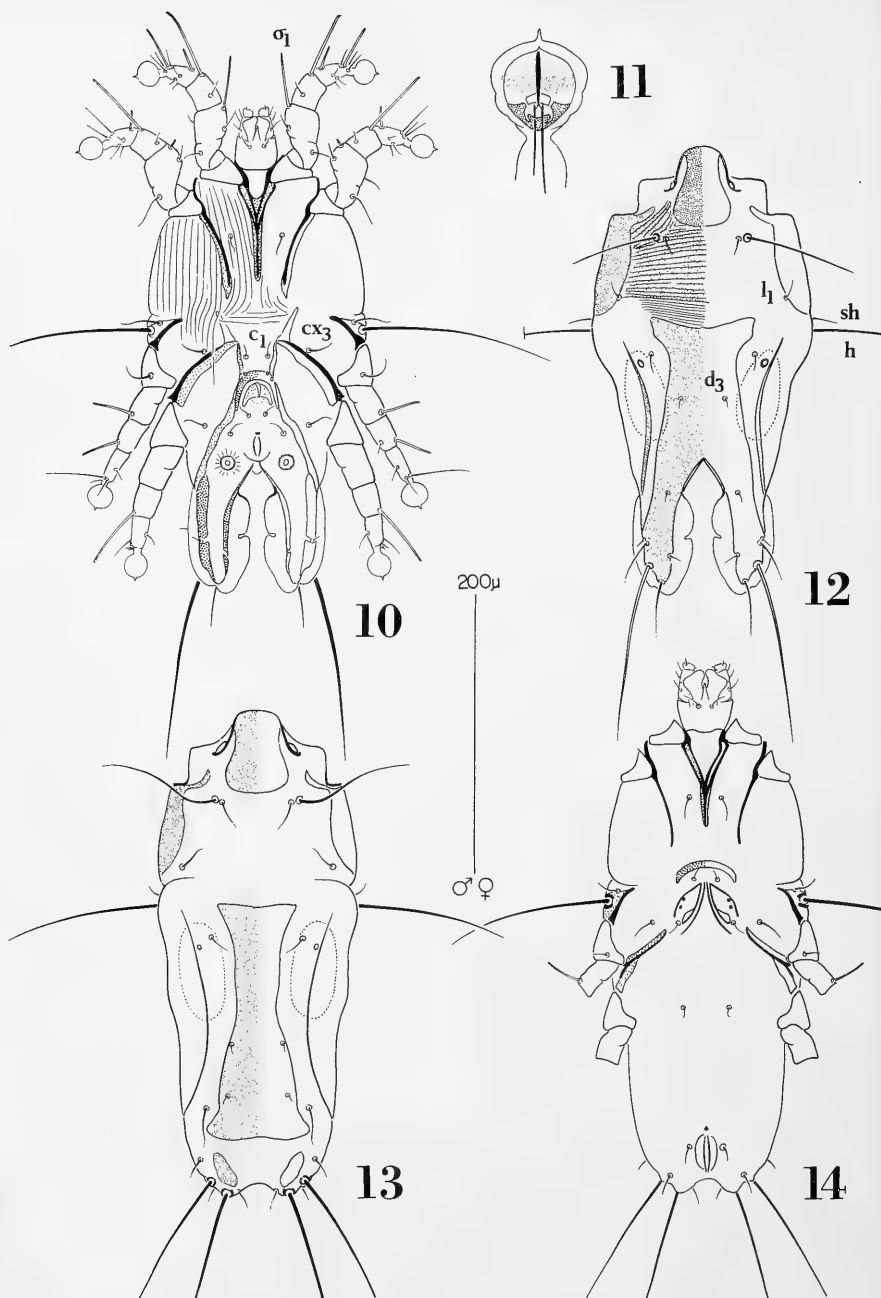


Fig. 10-14. *Parazumptia gallinulae* gen. nov., spec. nov.: ventral (10) and dorsal (12) aspects of male; enlarged pretarsus (11); ventral (13) and dorsal (14) aspects of female. Setae:  $c_1$ , central;  $cx_3$ , coxal;  $d_3$ ,  $l_1$ , dorsal and lateral hysterosomals;  $h$ , humeral;  $sh$ , subhumeral

Migratory Animal Pathological Survey team (MAPS) (NU 13,442); 2 ♂, same data as holotype except January 19, 1967 (NU 13,432); 5 ♂, 6 ♀, Bharatpur, Rajasthan, India, December 12, 1969, MAPS (UGA 6256). Holotype, paratypes: UGA; paratypes: AMNH, NMNH.

Remarks. The same specimen of *Gallinula chloropus* harboured *Zumptia macclurei* and *Parazumptia gallinulae*. The former mite species was not found on other specimens of the moorhen infested with *P. gallinulae*.

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HARVARD  
UNIVERSITYUITGEGEVEN DOOR  
DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING

## REGISTER VAN DEEL 119

\* Een sterretje duidt een naam aan, welke nieuw is voor de wetenschap.

\* An asterisk denotes a name new to science.

Uit het register zijn weggelaten de namen uit het artikel van Van Lith, welke reeds zijn opgenomen in het eigen register (p. 122).

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